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THE BIOLOGY OF REEF-BUILDING CORALS

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WITH SIX PLATES.

CONTENTS.

1. INTRODUCTION.

The aim of this paper is to survey knowledge on the biology of reef-building corals. Data on the physiology, adaptations and life-history of corals and, as far as this is relevant, that of associated organisms, have been brought together so as to demonstrate the relationship of corals to their physical and biological environments. Although this paper is based on the work of the expedition, information has been drawn from all regions in which coral reefs occur. The pioneer work of Vaughan on the physiology and adaptations of corals, summarized in reviews published in 1919 and 1930, has been of especial value, and also that of Gardiner, Wood-Jones and Sewell in the Indian Ocean, of Boschma, Umbgrove and Verwey in the Dutch East Indies, of Mayor at the Tortugas, Mer Island and Samoa, of Crossland at Tahiti and the Red Sea, and the recent work of the Japanese at the Palao Tropical Biological Station in the Pelew Islands. The essentially geological problem of the origin of the submarine platforms on which coral reefs have been formed lies outside the scope of this paper.

An opportunity is provided for recording observations made in regions of the Great Barrier Reef not visited by the Shore Party, namely the islands and reefs of the Torres Strait, especially the Murray Islands, which were visited during April and May, 1929, and the Capricorn Islands on which a few days were spent in August, 1929. Important information was also obtained during later visits to coral reefs on the Hawaiian Islands (October, 1929), Bermuda (September, 1931), the Dry Tortugas (July–August, 1934) and the Bahamas (September, 1934). The visit to the Tortugas was of especial value. Research which has assisted in the preparation of the paper was carried out and Atlantic coral reefs examined on the site of the pioneer researches of Mayor, Vaughan and their associates. Acknowledgments are due to the Carnegie Institution of Washington and to the Royal Society of London for the hospitality and financial aid which made this visit possible.

2. CHARACTERISTICS OF CORAL REEFS.

Biologically considered coral reefs may be defined as marine communities found only in shallow tropical waters,* the dominant organisms being Madreporaria containing zooxanthellae (*i.e.* "reef-building corals") together with certain Hydrocorallinae and Alcyonacea which also form stout calcareous skeletons and contain zooxanthellae. In the Atlantic, but not in the Indo-Pacific, Gorgonacea are also important elements in the formation of reefs. Owing to the exceptional powers of skeleton formation possessed by the majority of these organisms, massive reefs have been constructed which provide surface and shelter for a varied assemblage of other organisms. Some of these, notably Foraminifera and Mollusca amongst animals and nullipores amongst plants, assist materially in the formation and consolidation of reefs. Others bore into coral rock and so assist in the disintegration of the reefs.

After initial establishment on a suitable marine platform the subsequent upward growth of reef-building corals gradually brings these and the reef mass they have constructed within the influence first of wave action, influenced profoundly by the action of prevalent winds, and finally, during periods of low tide, of exposure to the air. The subsequent formation of islands on many reefs is probably due to the negative displacement of sea-level.

This upward growth of reefs has had important effects on both the individual corals and on the reef mass which they form. The corals, by their own powers of skeleton formation, have exposed themselves to shore conditions even in regions remote from any land mass. In the course of time many species of Madreporaria have become adapted, both morphologically and physiologically, to withstand these conditions. These adaptations have not been acquired by all reef-building corals, nor to the same extent by all those which do possess them. The zonation of coral species revealed by the ecological

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* The phototropic zone of Gardiner (1936).

surveys of Mayor (1918*a*) at Mer Island and (1924*a*) at Samoa, of Baker (1925) in the New Hebrides, of Manton (III, 10*) at Low Isles and of Abe (1937*b*) at Palao is the result of this varying degree to which corals are adapted for withstanding extremes of temperature, salinity and of exposure to sediment and to the air which is involved in life between tide-marks on the upper surfaces of reefs.

The upward growth of a reef is limited by exposure to the air but its general form is moulded by wave action. By the resistance it offers to wave action the reef itself creates different environments on its exposed and sheltered faces. Apart from fringing reefs, which are bounded on the one side by a land mass and thus exposed to wave action only on their seaward slopes, this asymmetry is the result primarily of the action of seas driven by the constant force of prevailing winds. This moulding action of the sea was first described for the outer reefs of the Great Barrier by Paradice (1925). He showed that the reefs are crescentic in shape with the convexity directed towards the Pacific swell. The summits of the reefs, consisting largely of flat expanses of dead coral rock cemented by Lithothamnion, lie on the seaward side. On this side the reef descends steeply into deep water but only gradually on the inner side, where flat-topped pinnacles of rock clothed with living coral rise from a sandy bottom almost to the surface. Paradice's paper is illustrated with diagrams but most effectively with an aerial photograph of Coates Reef. He adds that the seaward edge of the reef, just below low-tide level, is covered with living coral, the reef thus growing outwards against wind and weather. This is universally true of virile coral reefs.

The work of the Shore Party confirmed and extended these preliminary observations of Paradice. In their account of Yonge Reef, one of the Outer Barrier series, they distinguished the following areas in order from the seaward to the sheltered side: outer ridge, outer moat, reef crest, inner moat, boulder zone, anchorage coral zone, zone of coral heads (Stephenson, Stephenson, Tandy and Spender; III, 2). Analysis of Low Isles and similar low wooded islands lying in the channel between the Barrier and the mainland revealed conditions of greater complexity, primarily due to the greater height of these reefs, but in essentials they are similar while the moulding action of the trade winds is most striking. This is revealed by an examination of the map of Low Isles (III, 2) and of the wind rose printed upon it.

Apart, therefore, from adaptations for shore life, different genera and species of corals are adapted for life in the diverse environments found between the seaward and sheltered sides of reefs. For the purposes of this paper only the three main regions can be considered, but the presence of the various sub-environments must be borne in mind. These main regions are (1) the outer ridge exposed to the full force of the sea, (2) the reef crest on which the surf breaks at low tide, and over which at all times water swirls with great force, and (3) the sheltered area in the lee in which grow pinnacles of living coral with sandy areas in between. The adaptation which fit corals for life in these regions will be considered.

The Madreporaria, as their ubiquity and vast abundance in suitable areas in tropical seas bear witness, are amongst the most successful of marine invertebrates. This is due, apart from their obvious powers of skeleton formation, to less obvious, but equally significant, powers of adaptation. Species have been evolved capable of flourishing in all the varied conditions which the animals themselves bring into being by their unique powers

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* Papers published in these reports will be referred to in this manner throughout, the author's name being followed by the volume number in roman numerals and the paper number in arabic numerals.

of skeleton formation. An initial capacity for the building of reefs has raised problems of existence which subsequent adaptation has solved.

Analysis of the biology of reef-building corals must therefore be concerned both with corals as individuals (usually colonial) and as reefs, *i.e.* as marine communities with the capacity for providing a series of widely different habitats for their constituent members. A study of the individual must include physiology, notably feeding, digestion and respiration, and also adaptations and life-history. That of the reefs as communities involves consideration of the significance of the zooxanthellae, of the formation and maintenance of reefs and of the factors governing their distribution, both horizontal and vertical.

3. NUTRITION.

It has been shown (Yonge: I, 2) that, despite certain previous statements to the contrary, corals are specialized carnivores, all species of forty genera of Madreporaria examined being adapted in various ways for the capture of zooplankton. Later examination of Atlantic corals at the Tortugas confirmed this conclusion which had previously been reached by Vaughan (1919*b*). The findings of Abe (1938), who examined 16 species of corals at Palao, are similar. The distended tentacles of an expanded coral colony constitute as effective a mechanism for the collection of zooplankton as do the ciliary feeding mechanisms of the members of a bed of lamellibranchs for the collection of phytoplankton. This is clearly demonstrated by the photographs, kindly supplied by Prof. T. A. Stephenson, of expanded *Turbinaria* and of a colony of *Favia*, in the contracted and expanded condition, reproduced in Plates I and II.

It was also shown that the tentacles never accept vegetable matter, and that the mouth never swallows this (Yonge: I, 2), while the digestive enzymes in the coelenteron are incapable of acting upon it (Yonge: I, 3). The enzymes are those of a specialized carnivore. Criticisms based on the frequent absence of food from the coelenteron were refuted. Corals feed by night and digest zooplankton rapidly, usually disgorging the empty skeletons within twelve hours (Nicholls: I, 3), hence the coelenteron will normally be empty when animals are collected by day. Finally the validity of the argument that the cavity of the calix is frequently too small to permit the entrance of food was examined. It was found (Yonge: I, 2) that the polyps expand high above the skeleton, especially in species where the calix is blocked by a large columella, and in addition that certain species digest extra-coelenterically by extrusion of the mesenterial filaments which wrap round the prey.

There is thus nothing in the structure or physiology of reef-building corals to prevent zooplankton from being the sole source of nourishment. But it has long been a subject of controversy as to whether or no the zooplankton in coral reef waters is sufficiently abundant to supply their needs. Those who deny that it is sufficiently abundant regard the contained zooxanthellae as at any rate an accessory source of nourishment. The protagonists of the two views are listed elsewhere (Yonge: I, 2). This contention raises two questions. First, what amount of zooplankton is actually available in such areas, and second, what evidence is there that corals are able to obtain nutriment from the zooxanthellae?

The only worker to make quantitative examinations of the available zooplankton in coral reefs prior to the Great Barrier Reef Expedition appears to have been Krämer (1897), who worked in Samoan waters between 1893 and 1895. It is noteworthy that he decided that zooplankton was adequate to supply the needs of the corals. Russell (II, 6), using modern methods, has compared the abundance of zooplankton in the Barrier Reef lagoon with that of the following regions in northern European waters: Anholt Knob (Cattegat), Smith's Knoll and Borkumriff (North Sea), and Varne and Sevenstones (English Channel). Reference should be made to his paper for full details, but he gives abundant evidence for his considered conclusion that "the Barrier Reef zooplankton is as rich numerically when averaged over the year as that of those northern regions compared." A totally misleading impression is gained when we consider, as we are very apt to do, the figures for the spring increase in northern waters neglecting the equally low winter figures. In Barrier Reef waters there is little seasonal difference. It is true that the phosphate figures are uniformly low, averaging 5 mg. of phosphate per cubic metre (Orr; II, 3), but there is, on the other hand, a perpetual mixing of waters owing to the action of the trade winds which prevent the formation of a thermocline in the enclosed waters within the Barrier. Hence nutrient salts in all layers of the water are available for plant life. Unlike areas of similar depth in temperate waters, such as the English Channel, a significant proportion of the nutrient salts is never immobilized in deep waters inaccessible to the phytoplankton near the surface. Phytoplankton production in the waters within the Great Barrier Reef proceeds with maximum efficiency throughout the year. Marshall (II, 5) has shown that, although numbers are low, they vary little throughout the year. There is also the possibility discussed by Orr (II, 3) that there is some upwelling of water, rich in nutrient salts, along the outer edge of the Barrier which may cause a continual enrichment of the lagoon waters.

Further, as emphasized by both Russell and by Orr, the high temperatures, ranging from 21·24° C. to 29·88° C., will, by their effect on the metabolism of planktonic organisms, produce rapid development, and so a quick succession of new generations. Thus phytoplankton will multiply quickly, while the loss of many of the zooplankton organisms taken as food by the corals and other carnivores will soon be made good by the development of eggs and larvae liberated by the survivors. Replacement is probably at least two or three times quicker than in north temperate waters. The same point is made by Hardenberg (1938) in a review of fishery problems in the Dutch East Indies. He points out that smaller planktonic eggs may hatch within twelve hours, while the absence of low winter temperatures is reflected in the constancy throughout the year of the planktonic population, which he estimates at one-third to one-quarter that of the North Sea. The popular idea of the great richness of tropical seas has no basis in fact as far as economic fisheries are concerned, although, as Hardenberg states, low total production is to some extent made good by accelerated growth.

Phytoplankton will be of value to corals only to the extent that it nourishes the zooplankton on which they feed. Bottom-living animals which feed by ciliary or setous mechanisms compete directly with the zooplankton in their demands on the phytoplankton. By far the most important of these are the Lamellibranchia. But although there is a great wealth of species on the reefs (see Iredale; V, 6), the only lamellibranch which occurs in numbers remotely comparable with the dense beds of mussels, oysters or clams in temperate seas is the small rock oyster, *Ostrea mordax*, which occupies a restricted zone near high tide mark corresponding to the *Balanus* zone in temperate seas. The Tridacnidae which, in bulk of tissues, are the most important of the Lamellibranchia, are nourished to a large extent by their contained zooxanthellæ (Yonge; I, 11). Further, these animals are confined to the surface and sides of reefs, the muddy bottom of the lagoon channel being almost devoid of life. It is possible that only in shallow water are bottom-living animals able to compete with the zooplankton. There is probably little surplus phytoplankton left to sink to the greater depths of the lagoon channel. The general impression gained was that bottom-living invertebrates here obtain a relatively smaller proportion of phytoplankton than do those in temperate seas.

There remains for consideration the competition to which corals are subjected in their demands in the zooplankton. Russell (II, 6) has calculated the proportion of predaceous members of the zooplankton to those which feed directly on the "producers" (phytoplankton and certain Protozoa). They average 5% as compared with 3·1% for the Borkumriff in the North Sea. But many of these, notably Chaetognatha, larval Stomatopoda and probably fish larvae, will be eaten in their turn by corals and similar bottom-living carnivores. Personal observations, covering a wide area, confirm Russell's tentative opinion that the shoals of atherines and other sardine-like fish which certainly feed on zooplankton, although they may occur locally in great numbers, notably around Mer Island, cannot be compared in numbers and feeding capacity with pelagic fishes in temperate waters. Hardenberg (1938) points out the relative paucity of fish in East Indian waters.

Amongst bottom living animals competition will be experienced from other Coelenterata, notably Alcyonacea and species of *Palythoa*, but, although these cover large areas (see ecological report; III, 2), they cannot be compared in bulk to the Madreporaria. Hydroids are few in number and so, unlike the Atlantic reefs, where Madreporaria are less abundant, are gorgonids.

There appear to be adequate grounds for the statement that Madreporaria obtain the great proportion of the available zooplankton in the waters which bathe coral reefs. They obtain this because they are more highly and variously specialized for its capture than are their competitors. Moreover, although a coral reef presents a vast surface of living matter, this actually constitutes no more than a thin film over the surface of the massive skeletons it forms. In other words, the food requirements of corals are a great deal less than they appear to be, while the ratio of feeding surface to body volume is certainly not exceeded, and probably seldom approached, throughout the remainder of the animal kingdom.

4. ADAPTATIONS OF REEF-BUILDING CORALS.

The major problems of life presented to sedentary animals living in shallow water are those concerned with feeding, with exposure to water movements and falling sediment and also, for those which live above low-water mark, with exposure to the extremes of physical conditions involved in life in the littoral zone. Problems concerned with reproduction will be considered later. Reef-building corals have been adapted in a variety of ways, both morphologically and physiologically, to enable them to solve these problems, and although adaptations for different purposes necessarily overlap, it will be most convenient to discuss them under the various headings indicated above.

(*a*) ADAPTATIONS FOR FEEDING. It may reasonably be assumed that, so far as feeding is concerned, solitary corals (excluding the Fungids) exhibit a more primitive condition than colonial species, and that the deep- or cold-water corals are less specialized than the majority of the reef-builders. The former, whether they be imperforate, such as *Flabellum* or *Caryophyllia* (both solitary) and *Lophohelia*, or perforate, such as *Balanophyllia* (solitary) and *Dendrophyllia*, have large polyps and a relatively small skeleton. Feeding is exclusively by means of the tentacles and cilia are concerned exclusively with cleansing. This applies also to many of the reef-builders with massive skeletons, notably the astraeids and the larger polyped maeandrines as described originally by Carpenter (1910) for *Isophyllia*. But in many of the reef-builders the polyps are small and very numerous. Many of these, *e.g. Seriatopora*, *Pocillopora*, *Stylophora*, *Leptastrea*, *Cyphastrea* and *Porites*, have upwardly directed ciliary currents on the column and the outer sides of the tentacles (Yonge ; I, 2). This is also true of many of the Agariciidae, *e.g. Psammocora* and *Pavona*, where there is no column. In all these genera food captured by the nematocysts on the coenosteum is thus conveyed to the tentacles by cilia. The process is taken still further in two other genera of the Agariciidae, *Coeloseris* and *Pachyseris*. In the former all material falling on to the surface of the colony is carried to the polyps by cilia, the tentacles merely assisting to a minor degree and never selecting material for passage to the mouth. In *Pachyseris*, as confirmed recently by Abe (1938), tentacles are absent, their role in food capture being played by the extruded mesenterial filaments. Material is carried over the ridged surface of the colony by ciliary action. Abe (1938) states that ciliary reversal occurs in *P. speciosa* but, although the possibility of this was realized, it was not observed in *P. torresiana* (Yonge ; I, 2).

Ciliary reversal certainly occurs in a number of corals as it does in the actinian, *Metridium* (Parker, 1896, 1905, 1928 ; Parker and Marks, 1928). In all corals in which it was found its presence was correlated with the size of the tentacles, which were too small to carry food to the mouth. This applies to the maeandrines, *Tridacophyllia lactuca* and *Merulina ampliata*, and to all fungids examined, species of *Herpetolitha*, *Döderleinia* and *Fungia*, with the exception of *F. actiniformis* var. *crassitentaculata*, where alone the tentacles are long. On the other hand, Abe (1938) states that in the very similar species, *F. actiniformis* var. *palawensis*, reversal occurs in the disc region round the mouth. It is possible that both in this case and in that of *Pachyseris* mentioned above Abe may have been misled by the formation, on the stimulation of food, of mucous strings which are caught by the inwardly beating cilia on the stomodaeum, and so give the appearance of reversal of cilia on the disc over which the mucus strings are pulled. This certainly explains the statements of Vaughan (1913, 1919*b*) that ciliary reversal occurs in *Maeandra areolata*. This species, which was examined at the Tortugas, has large tentacles and no evidence of reversal was found (Yonge, 1935*b*).

The substitution of small and numerous for large and fewer polyps may have been advantageous to the many reef-builders which possess them by providing a more efficient means of capturing the many minute zooplankton organisms of tropical seas. The assistance of cilia, although not universal, being absent for instance in *Acropora* and *Montipora*, has also probably assisted by increasing the possible feeding surface. But it entails a loss of efficiency in cleansing and, for reasons given below, is confined to species which live at or near the surface of reefs where the water is constantly agitated. Reversal of cilia, which occurs solely on the stimulus of material of animal origin, does not affect the normal cleansing action of the cilia.

The great majority of reef-building corals expand only by night. A short list of those which do expand by day has previously been given (Yonge ; I, 2) but a more complete statement on this subject has been kindly prepared by Prof. T. A. Stephenson who, being especially concerned with field work on the reefs, had exceptional facilities for observing corals in nature. This statement forms an appendix to this paper. It should be noted that essentially deep- and cold-water corals expand by day. This is true of *Dendrophyllia nigrescens* (Low Isles), *Balanophyllia regia* (Plymouth, see photograph reproduced in Yonge, 1932), *Caryophyllia smithii* (Plymouth) and *Lophohelia prolifer* (Trondhjem, Norway). Abe (1939*a*) has recently investigated experimentally this problem of expansion and contraction of the polyps in *Caulastraea furcata*. He shows that they begin to expand about 20 to 25 minutes before sunset and to contract about 30 minutes before daybreak, the time for each process being from 15 to 18 minutes. When expanded the polyps react to mechanical and chemical stimuli, several adjacent polyps reacting as well as the one actually stimulated. There is no fundamental rhythm, polyps expanding when exposed to darkness in the daytime and contracting when exposed to light during the night. He also found that, although the stimulus of food will not cause expansion in light, this is brought about when corals are placed in water of low oxygen and high carbon dioxide tension. From this he concludes that " expansion and contraction of the polyps of some corals is directly related to light and darkness, and expansion of the polyps is probably related to gas metabolism, especially to diffusion of carbon dioxide." The latter he considers due to the accumulation during the night of carbon dioxide in the tissues owing to the absence of photosynthesis by the zooxanthellae. But this implies that it is expansion by night which requires explanation, whereas it is actually the contraction by day which represents the difference in behaviour between reef-building corals and other Coelenterata. Actinians and alcyonarians all expand by day, and so, as already noted, do the deep- and cold-water corals. Certainly gaseous diffusion will be more efficient when the corals are expanded, while the presence of the zooxanthellae, which both remove carbon dioxide and supply oxygen during the daytime, will certainly counteract any ill-effects of contraction by day. Abe has shown what happens when the surrounding water is artificially lowered in oxygen and increased in carbon dioxide content. This may be interpreted as a physiological reaction permitting greater gaseous exchange. His results, interesting and suggestive as they are, do not solve the fundamental problem as to why the polyps of the majority of reef-builders contract by day. Available knowledge only permits the speculation that this is a direct effect of the intense light to which reef-building corals, by their heliotropism and existence within the tropics, expose themselves. In general the tissues of the other reef-inhabiting Coelenterata are more deeply pigmented (this also applies to *Dendrophyllia*), and so are more effectively screened from the harmful effects of light. The various species of *Tridacna* which are always fully expanded by day in shallow water, exposed to the intense light of the tropical sun, are conspicuous for the intense pigmentation of the thickened and flattened mantle edges in which the zooxanthellae are contained (Yonge ; I, 11).

(*b*) FORM OF THE SKELETON IN RELATION TO WATER MOVEMENTS.—It has long since been known that, in general, the more solidly built corals, such as astraeids, maeandrines and the more massive species of *Acropora* occur on the exposed seaward slopes of reefs, and the more delicate, branching and foliaceous species in sheltered water in the lee (Darwin, 1889 ; Wood-Jones, 1912 ; Vaughan, 1919). But this statement requires some qualification. Stephenson, Stephenson, Tandy and Spender (III, 2) state, with reference to the coral fauna on the outer ridge at Yonge Reef, that " the corals include massive species, some of them growing to large size, and species of *Acropora* of certain styles of growth. These latter may form wide dish-like brackets or expansions (*A. hyacinthus*), encrusting sheets yards in extent (*A. palifera*), systems of heavy branches closely applied to the substratum (*A. decipiens*); or may consist of very short massive cones united to a firm foundation (*A. gemmifera*). Apart from these more or less solid forms, a totally different species (*A. delicatula*), occurring particularly on the sides of clefts, makes small rounded bushes of branches so slender and brittle that an entire specimen can with difficulty be obtained —yet this form can withstand the breakers."

Illustrations of massive species in such localities are given in Plate III, figs. 4 and 5. The first of these photographs was taken on the seaward side of Michaelmas Reef, the second on the seaward edge of Ruby Reef, one of the Outer Barrier series. Plate IV, fig. 6, shows *Acropora* growing on the seaward slope at Northwest Island Reef, one of the Capricorn Group. This photograph, taken at a time of exceptionally low water, reveals the sudden drop beyond the outer ridge.

Corals of the reef crest are typically low and often encrusting, and are scattered somewhat sparsely. At Yonge Reef the Shore Party (III, 2) reported that species of *Acropora* were dominant, two especially with low bushy growths, and one with a cyathiform structure with a stout stalk and short branches on top. The floor of shallow pools in this cemented region may be encrusted with a wide variety of species of many different genera. The general appearance of the cemented reef crest at Northwest Island reef is shown in Plate V, fig. 8, and the varied coral fauna of a pool in this region in fig. 9.

In the sheltered water in the lee the delicate branching species occur in great abundance, such as the stagshorn *Acropora*, the more delicate species of *Pocillopora* and *Seriatopora hystrix* (extremely abundant in the lee of the lithothamnion ridge on the outer reef at Mer Island as originally described by Mayor (1918*a*)). Many foliaceous species, *e.g.* of *Echinopora*, *Pavona*, *Montipora* (see Plate IV, fig. 7) and *Turbinaria* occur. The general appearance of this region when fully exposed is shown in Plate VI, figs. 10 and 11. On the sandy patches in the lee of reefs and in the standing water of the various moats are found unattached corals, species of *Fungia*, *Herpetolitha* and *Döderleinia*. Abe (1937*b*) has described the aggregation of *Fungia* in such regions owing to water movements. In the Atlantic this particular niche is filled by the maeandrine, *Maeandra areolata* (Yonge, 1935*b*).

While in general the form of a coral shows close agreement with the intensity of water movements in the regions where it normally occurs, there has long been a controversy as to the extent to which, within any genus, these different forms are true species or merely growth forms. Hickson (1898) came to the opinion that the hydrocoralline, *Millepora*, consists of the one species only although there are many growth forms. Crossland (1928*b*) describes and figures five facies at Tahiti, all of which directly respond to external conditions as Hickson postulated. Wood-Jones (1907, 1912) extended this view to cover the Madreporaria, while Vaughan (1919*b*) gave support to this with the aid of photographs showing differences in the growth form of *Stylophora pistillata* in deep calm waters and shallow agitated water at Mer Island and of *Porites porites* from different environments at the Tortugas. Stephenson and Stephenson (III, 7) came to the general conclusion that "species in the ordinarily accepted sense of the term do exist in many coral genera in considerable number, and that many of them are fairly easily recognized in the field: and that Wood-Jones has considerably overstressed the effect of environmental conditions on the corals, although such an effect certainly exists, and is responsible for a considerable range of variations." Dr. J. Verwey informed the author personally that, after his long experience on the coral reefs in the Bay of Batavia, he had no difficulty in recognizing, both in the field and in the museum, a wide range of species of *Acropora*. Umbgrove (1939*a*) states that Verwey is describing 21 species of *Acropora* from this region.

Coral growth is certainly affected by water movements.* Mayor (1924*c*) describes the exceptional size of coral colonies growing some distance below the breakers off the seaward edge of Aua Reef, Samoa. Stephenson and Stephenson (III, 7) conducted experiments in which they divided coral colonies, keeping one half in the moat at Low Isles and the other half in the anchorage. They found that species normally inhabiting the moat grew equally well in both areas, but that species from the anchorage either died under the more stringent conditions in the moat or failed to grow so well. Crossland (1931, 1935) has described the reduced building power of many species of astraeids at Tahiti, although the precise reasons for this remain to be determined. In the course of work at the Tortugas (Yonge, 1935*c*), it was found that the typical flattened colonies of *Siderastrea radians* from the beach rock exposed to the surf gave place, in the still, sediment-laden waters of the moat at Fort Jefferson, to rounded colonies with larger calices usually with a complete fourth cycle of septa. All stages between this type and the flattened type outside with an incomplete fourth cycle of septa were found, the calices even varying within the same colony. At one time the moat was in free communication at two points with the sea and was scoured clean. Since the wall was breached in 1919 one of these has been blocked and the moat has become a sediment trap, with the result that the great majority of the coral species originally listed from this region by Vaughan (1918*b*) have disappeared. The survival of *S. radians*, now most abundant there, was judged due to its capacity for modifying the form of the skeleton. Recently Abe (1937*b*) has shown that current force influences the direction of the branches of some corals, notably *Millepora alcicornis*, *Montipora tortuosa*, *M. ramosa*, *Porites compressa*, *P. nigrescens*, *P. cylindrica*, *Pachyseris rugosa* and, less often, *Seriatopora caliendrum*. The branches tend to develop parallel to the direction of the current.

To quote a previous statement (Yonge, 1935*c*), "The great success of the Madreporaria, which is so forcibly demonstrated by the wide-spread occurrence and immense size of coral reefs, may not unreasonably be attributed to the presence within the group of species highly specialized for a particular environment, and others capable of wide modifications in form which enable them to adapt themselves for life in a variety of different environments. The acceptance of this view would certainly explain, and perhaps tend to allay, the conflict between those who believe in the validity of the great number of species of Madreporaria which have been described and those who regard the majority of these as no more than growth forms."

(*c*) THE EFFECT OF SEDIMENT. Modern research has tended to discount to some extent the once widely held opinion that coral growth is impossible except in very clear water. Falling sediment certainly represents one of the great dangers to which corals are exposed, but the animals are highly specialized for removing it from the coenosteum by means of the cilia with which this is covered. Marshall and Orr (I, 5) are the first to study the matter quantitatively. They found that, as a rule, corals with large polyps are more efficient in cleansing than those with small polyps unless the latter are finely branched. This agrees with observations noted above (Yonge; I, 2) that in many of the latter the ciliary currents assist in feeding with consequent loss of efficiency as agents

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* Credit should be given to Semper (1890) for first pointing out the importance of this factor in coral growth.

of cleansing. This is especially true of the Agariciidae. *Coeloseris mayeri*, which was studied at Mer Island where it occurs only near high tide marks, relies exclusively on water movements for cleansing (Yonge ; I, 2). This coral was not available for examination at Low Isles, and there Marshall and Orr found that *Porites* was the most susceptible to falling sediment, both in nature and in the laboratory. At the same time they do not think that the flattened tops characteristic of many colonies of *Porites* are always or even mainly due to the effect of falling sediment. At Low Isles certainly exposure appears to be the cause, as confirmed by Manton (III, 10) and later by Moorhouse (1936), who studied the manner of death of colonies of *Porites* exposed at low water following the lowering of the water in the moats after the cyclone of 11th March, 1934. On the other hand Abe (1937*b*) considers that similar colonies of *Goniastrea aspersa* at Palao are due to the effect of sediment.

The most efficient of all corals in the removal of sediment are the unattached species which may in stormy weather be buried under the surface of the sand on which they lie. Wood-Jones (1912) originally noted the efficiency of *Fungia* in this respect, while Marshall and Orr (I, 5) showed that it is actually able to uncover itself when completely buried, the process being admirably illustrated in a series of photographs. They ascribed the process purely to ciliary action, but Abe (1939*b*) has recently shown that in *Fungi actiniformis* var. *palawensis* this is brought about primarily by expansion of the disc tissues, this cleansing process occurring rhythmically. By the same agency the animal is also able to right itself when turned over (as it frequently may be in stormy weather). Expansion of the disc tissues for cleansing and uncovering has already been described by Yonge (1935*b*) for *Maeandra areolata* in the Atlantic. Water is taken into the coelenteron and the tissues may be raised above the skeleton by as much as 2 cm. although the tentacles do not expand, feeding being impossible under these conditions. The process of uncovering when buried to a depth of at least 2 mm. took some 10 hours. Comparative experiments revealed that *M. clivosa*, which forms encrusting masses on rocks and on which sediment will tend to collect, removes sediment less efficiently than *M. areolata* but more efficiently than *M. strigosa*, which forms rounded colonies on which sediment will tend to fall off by the action of gravity. Cilia are aided by tissue distension in *M. clivosa*. As suggested by Marshall and Orr (I, 5), expansion of the tissues at night also probably assists in the removal of falling sediment.

The rounded colonies of *Siderastrea radians* from the moat at Fort Jefferson (Yonge, 1935*c*) removed sediment quicker than the flattened colonies from the beach rock. Specimens of the latter placed in the moat were soon covered with sediment which, unaided by water movements, they could not remove. Survival of this species in these still, sediment-laden waters appears due to change in form of the colony and of the calices. This is the direct effect of life in this environment and is not genetic, because all gradations between the two forms occur.

The majority of reef-builders are certainly well equipped for dealing with falling sediment. The reefs in the Bay of Batavia actually arise from a muddy bottom as originally described by Sluiter (quoted by Umbgrove, 1928), who thought that corals first established themselves on solid objects such as shells, and especially pieces of waterlogged pumice. More detailed descriptions of these reefs are given by Umbgrove (1928) and Umbgrove and Verwey (1929). There is, of course, a limit to the concentration of sediment which can be withstood by corals ; for instance, reefs are absent in the Eastern part of the Bay of Batavia where the River Tjitaroem discharges great quantities of silt. But even under these conditions the prime danger of corals comes from encroachment of accumulated silt over the basal tissues, as emphasized by Marshall and Orr (I, 5) and Moorhouse (1936). Mayor studied the effects of burial under mud of corals both at Mer Island (1918*a*) and the Tortugas (1918*b*), and Edmondson (1928) made similar experiments at Hawaii. They found that corals which live near high tide mark can withstand the effects of this longer than those which live only in the cleaner conditions near low-water mark and below. But for survival all must be uncovered by water movements within a relatively short time; only the unattached fungids and *Macandra areolata* are capable of uncovering themselves by their own activities.

(*d*) ADAPTATIONS TO SHORE CONDITIONS.—These involve physiological adaptations, common to all shore-living animals, which enable them to withstand extremes of temperature and salinity and of exposure to the air involving danger of desiccation. Mayor (1918*b*) found that, of a series of eight Tortugas corals, *Acropora muricata* was killed at 34·7° C., while *Siderastrea radians* survived until 38·2° C., the other species dying at intermediate temperatures. This agrees well with the habitats of the species, those living nearest high-tide mark resisting the highest temperatures. Edmondson (1928) found similar correlations between habitat and ability to withstand high temperatures at Hawaii. Mayor ascribed death to accumulation of carbon dioxide in the tissues, species with the highest metabolism dying first. But, as will be shown later, the data on which he based his estimates of metabolic rates cannot be accepted, while he overlooked the effect of photosynthesis by the zooxanthellae. High temperatures would occur only by day when the algae would automatically remove carbon dioxide. There seems no reason to look further than physiological adaptation for the explanation of these different lethal temperatures.

With regard to salinity, Mayor (1918*a*) found that at Mer Island only *Coeloseris mayeri* (a typical shore species already reported as depending on water movements exclusively for cleansing), *Porites murrayensis* and *P. mayeri* could withstand 24 hours' exposure to 50% sea water. Vaughan (1919*b*) found that, of 17 species of Tortugas corals exposed for 24 hours to the same salinity, all were damaged or killed except *Macandra areolata*, *Porites asteroides* and *Siderastrea radians*. But none was damaged in water of 80% salinity. Wells (1932) found that only five species of Tortugas corals could withstand an increase as well as a decrease in salinity of 50%. Edmondson (1928) conducted experiments which indicated that "at least 3 or 4 species of Hawaiian corals are able to live for at least 3 months in solutions of sea water ranging from about 66⅔ per cent. to about 110 per cent." In all cases the resistant species were shore-living.

Mayor (1918*a*), Vaughan (1919*b*) and Edmondson (1928) all observed the powers of survival of corals when exposed to air. They agree that in general survival is a function of the porosity of the skeleton, but that corals from the inner reef flat are more resistant to exposure than those from exposed positions. The general effect of exposure in the levelling of the upper surfaces of reefs by stopping further upward growth is clear. At best corals have only a limited power of surviving exposure, especially when, during day low tides in the summer, this is combined with high temperatures. Many reef corals were killed at Low Isles in the summer during such conditions.

Data on none of these factors is very complete, but combined they do indicate that the power of physiological adaptation is amongst the factors which have enabled Madreporaria to form reefs which break the surface at low water. In the varying degree to which species are adapted for shore life lies the explanation of the zonation of corals on the shore which has been noted by all who have studied the ecology of coral reefs.

5. SIGNIFICANCE OF THE ZOOXANTHELLAE.

Experimental investigation of this problem formed the subject matter of much personal work during the course of the Expedition (Yonge and Nicholls; I, 6; I, 7; Yonge, Yonge and Nicholls; I, 8). The zooxanthellae were shown to be highly specialized for life within the endoderm cells of corals and other coelenterates, never occurring free in the sea, and being carried from generation to generation by way of the egg and the planula. They possess no sexual stages and are enclosed in a relatively stout cellulose wall. It was shown experimentally that they obtain from the animal carbon dioxide during periods of light only, and at all times available phosphate and nitrogenous compounds. The phosphate content of the water surrounding reef-building corals decreased even when it was artificially increased to 50 mg. per litre. On the other hand with *Dendrophyllia*, which contains no zooxanthellae, there was a continuous increase in the phosphate content of the water owing to excretion by the animal. Similar excretion of phosphate was found in experiments with corals which had been largely deprived of their zooxanthellae by subjection to darkness for 152 days.

Zooxanthellae thus find protection within the tissues of the animal and also their inorganic food. Experiments indicated that they are normally at their maximum possible abundance within any coral colony, being limited only by the two factors of light and of available inorganic food salts. The influence of light was indicated by the fact that corals from deeper water contained fewer zooxanthellae than those from shallow water (Yonge, Yonge and Nicholls; I, 8). Corals occasionally found growing in the dark under boulders were light in colour and contained few algae. A number of such colonies were later seen in deep shade on the piles at the wharf at Fort Jefferson, Tortugas. Mr. L. L. Mowbray showed the author in 1931 an almost colourless colony of *Oculina diffusa* which had lived for at least two years in a very shady place in the aquarium at Flats, Bermuda. Corals were kept for five months in a large light-tight box on the reef flat at Low Isles (see Yonge and Nicholls; I, 6, pl. ii, fig. 7). Water was able to circulate freely through this and the corals survived but lost the great bulk of their algae. Under such conditions the zooxanthellae are ejected by way of the "absorptive" zone at the base of the mesenterial filaments. This region is excretory as well as absorptive, and is the only region of the animal where particulate matter is either taken into or ejected from the tissues (Yonge; I, 4). These conclusions have been confirmed by the work of Smith (1939) on association between zooxanthellae and the actinian, *Anemonia sulcata*.

The quantity of available inorganic food material depends on the state of metabolism of the coral. When this is high excretion will be correspondingly increased. When it is lowered by starvation (Yonge and Nicholls; I, 7), high temperature (Yonge and Nicholls; I, 6) or low oxygen tension (Yonge, Yonge and Nicholls; I, 8), the zooxanthellae are starved of their inorganic food salts. Consequently many die and are ejected. They appear, embedded in mucus, as brown masses which are extruded from the mouth. Later raising of the metabolism, *e.g.* when a coral subjected to high temperature recovers (Yonge and Nicholls; I, 6), is accompanied by an increase in the content of zooxanthellae due to repeated division of those which survived.

The association is, therefore, essential to the zooxanthellae which can live only within corals or similar animals. It is an example of an association between algae and animals where the former becomes finally dependent on life in the latter though without in any way exploiting the other partner in the association (Yonge, 1935*a*).

On the other hand, the association is certainly *not* essential to the life of *individual* coral colonies. Examples of corals living in darkness without zooxanthellae have already been given; Duerden (1902) has described other cases. The significance of the association to the corals is very difficult to assess, but possibly of fundamental importance. Three possibilities have been suggested: (1) The corals may obtain nutriment from the algae, either normally or under exceptional circumstances. (2) The oxygen liberated by the algae during photosynthesis may be a contribution of fundamental importance to the respiratory needs of the animals. (3) The rapid removal of waste products of metabolism may be of great importance to reef-builders.

Data have already been given indicating that corals are all highly specialized carnivores. Prolonged experiments in which corals were starved and fed under identical conditions in light and in darkness failed to reveal that they ever obtained any nutriment from the algae (Yonge and Nicholls: I, 7). The tissues actually began to decrease almost immediately, most strikingly in the case of *Fungia*. At the end of 73 days of starvation at least half of the calix was exposed owing to retreat of the disc tissue (see Yonge and Nicholls: I, 7, pl. ii, fig. 4). Throughout this period algae were steadily expelled instead of being digested, as postulated by a number of workers, notably Boschma (1924, 1925*a*, 1925*b*, 1925*c*, 1926). Essentially similar results have since been obtained by Smith (1939) working on *Anemonia*. In the Tridacnidae, on the other hand, where the animal " farms " the zooxanthellae (which differ in certain respects from those found in corals) in the extended mantle edges, the algae *do* form an important part of the food of the animal (Yonge: I, 11).

The significance of the oxygen produced by the algae, although certainly considerable in amount (Yonge, Yonge and Nicholls: I, 8; Marshall: I, 9) is more difficult to assess. Its possible importance has most recently been stressed by Verwey (1930, 1931*a*). On the basis of experiments carried out with *Acropora hebes* he calculated that an ordinary colony of a large *Acropora*, weighing several kilograms, would consume during a tropical night 250 c.c. of oxygen for every kilogram of its weight. He added: "According to such a calculation a reef of some thousands of kilos consumes hundreds of litres of oxygen during one night. And as we may say that the water around these reefs contains about five litres of oxygen per cubic metre, we understand that such a reef is able to deprive about 120 cubic metres of wholly saturated water of all its oxygen." He maintained, therefore, that the oxygen produced by the zooxanthellae owing to photosynthetic action during the daytime was essential for the respiratory needs of the corals at night. The validity of these conclusions naturally depends on the validity of the original figures for oxygen consumption. Mayor made estimations of the oxygen consumption of a variety of corals from the Tortugas (1918*b*) and from Samoa (1924*a*). In both cases he related the oxygen consumption to the actual amount of living tissue and he obtained very remarkable results. In the first set of experiments he found that *Acropora muricata* has a respiratory rate per unit of living tissue more than 18 times greater than *Siderastrea radians*, three other species examined coming in between. In the second set of experiments *Pocillopora damicornis*, which gave the highest figures, had a respiratory rate 5½ times that of *Porites* *andrewsi* with two other species coming in between. These figures have been accepted with surprisingly little question, although both Vaughan (1930) and Verwey (1931*a*) criticize them. As the latter points out, the figures for *Acropora muricata* are equivalent to those for active animals, such as fish or squids. But in any case so wide a variation in the oxygen needs of different species of corals, all of which live under essentially similar conditions, demands explanation. This would appear to be provided by the results of experiments carried out at the Tortugas (Yonge, 1937). These indicated that a large proportion of the apparent utilization of oxygen by corals is actually due to oxidation of the mucus secreted by them during the course of the experiment. This varies greatly in different genera, being exceptionally high in species of *Acropora*. Many of these literally drip mucus when removed from water, and are more difficult to keep in captivity than species of any other genus because this mucus collects round the branches and putrefies. Mucus secretion by *Siderastrea radians*, on the other hand, is low. Mucus secretion also increases at certain times, *e.g.* during planulation in the case of *Macandra areolata*. Cary (1918, 1931) found that in Alcyonarians the species with the greatest surface per unit weight have the highest apparent metabolism. These results may also be due to a greater production of mucus by the branched species.

It is thus impossible to accept at their face value figures which claim to represent either the absolute or the comparative rates of respiration in different corals, or general conclusions based on these figures. It is particularly unfortunate that Verwey, whose work on coral reefs has been so extremely illuminating, should have based conclusions on the oxygen needs of a coral reef on figures obtained from experiments with a species of *Acropora*. If the possible margin of error is as high as it is in *A. muricata* then the figures may actually be 18 times too high. But even if they are only three times too high his conclusions are materially affected. The significance of the oxygen produced by the algae must remain undetermined. In any case the presence of algae *within the tissues* of corals is not necessary for this purpose. If they were not in the tissues of the animals, excretion from these would permit the existence in the surrounding water of a correspondingly more abundant phytoplankton which would raise the oxygen content during the day. Moreover, corals are well able to withstand temporary lowering of oxygen tension. Experiments on a variety of corals showed that the oxygen content of the surrounding water can fall to between 40 and 50% saturation before the rate of respiration is affected (Yonge, Yonge and Nicholls; I, 8). In lower tensions the rate of respiration declines, but all available oxygen is finally utilized. These results have since been confirmed by Kawaguti (1937*a*). The possible importance of the zooxanthellae in permitting contraction of the polyps during the day has already been discussed.

There remains the possibility that zooxanthellae may increase the metabolism of corals by their action as automatic organs of excretion, removing as rapidly as it is formed nitrogenous and phosphoric waste, as well as the bulk of the carbon dioxide (with consequent effects on the pH within the tissues). This conclusion, reached in 1931, has since received some confirmation in the interesting work of Buchsbaum (1937). He grew cultures of embryonic chick connective-tissue cells mixed with cells of the green alga, *Chlorella pyrenoidosa*, and found that, in the light, both algae and tissue cells grew better than control cultures of algae and of tissue cells. In the conditions under which the cultures were grown, Buchsbaum concluded that the beneficial effect was probably due to removal of carbon dioxide and increased supply of oxygen. But the significant point is certainly the increased growth of animal cells which occurred in this artificial symbiosis. In corals increase in metabolism may have the most important effect of increasing the rate of skeleton formation. Data on the growth of corals, discussed later, reveal a remarkable power of calcium metabolism. This has made possible the formation and maintenance of reefs. The conclusion has been tentatively advanced (Yonge, 1931, 1935*a*) that the association between corals and zooxanthellae, essential to the plants, but certainly not to *individual* coral colonies, may be an indispensable factor in the necessarily great powers of growth and repair possessed by the marine *communities* known as coral reefs. Unfortunately experimental data on this subject, in particular comparative figures for growth under otherwise identical conditions in light and in darkness, is lacking, but there does exist a quantity of relevant data indicating a direct effect of *light* on coral growth.

6. THE EFFECT OF LIGHT ON CORAL GROWTH.

Dana (1890) suggested that, as temperature in the tropical Pacific would permit growth of reef-building corals to considerably greater depths than those in which they actually occur, vertical limitation might be due to diminution in light. Gardiner (1903*a*) associated this with the needs of the zooxanthellae on which he then thought that corals fed. Wood-Jones (1912), who observed that corals fed on animal matter, ruled out the influence of light on vertical distribution. Vaughan (1919*b*) observed that corals failed to grow in any number in the shady areas under the wharf at Fort Jefferson, Tortugas, although abundant on the peripheral piles. Light was the only factor that differed. He kept corals in a light-tight live car. Many died, although a few survived for 43 days. It is possible that either the car became too hot or circulation was defective because, in experiments at Low Isles (Yonge and Nicholls ; I, 6), a wide variety of corals survived in darkness for 152 days, the only fatalities being due to sediment, which accumulated in the still water within the box. But the corals were certainly not so healthy as those in light. Edmondson (1928) states that approximately 50% of Hawaiian corals died in 18 days when exposed to total darkness on the reef with normal water circulation and food supply, although he does not describe the experimental procedure. He concluded that sunlight is an important factor in the life of shallow-water corals. Mayor (1924*a*) made the following significant statement : " In many places in Samoa, as over the Taema Bank, where the water is constantly agitated by the Pacific swell and the bottom is clean, hard, and free from silt, the corals at depths of 8·5 fathoms grow only to about one-third the linear dimensions they attain in shallower water, and there are wide spaces between the heads, indicating unfavourable conditions. It looks as if some factor such as light may have a decided influence in determining the growth of corals." Verwey (1930, 1931*a*) has shown that in the Bay of Batavia the depth to which the living reefs descend varies between 7 and 15 metres in different islands. These differences he associates with the turbidity of the water, which is greatest where the depth of the living reef is least and *vice versa*. Apparently the sediment does not affect the corals because Verwey found that the quantity of this decreases with increasing depth. Verwey is satisfied that it is the reduction in light intensity which affects the corals, in his opinion by diminishing the amount of oxygen produced by the zooxanthellae. Sewell (1935) discusses the effect of light on coral growth at some length. He cites various descriptions of vertical and undercut faces on the exposed surfaces of reefs, and also on the mushroom-shaped pinnacles which, as already described, are so characteristic a feature of sheltered waters in the lee of reefs. These have usually been attributed to the effects of erosion. Sewell, however, points out that " the absence of growing corals on these undercut vertical walls of the reefs and pinnacles cannot be solely attributed to erosion of the basis; one agency that may prevent the growth of corals in such a situation is in my opinion probably the lack of sunlight due to the overhanging coral growth, but other factors may be involved." . . . " Where a reef has already attained a steep slope, especially in those cases in which the reef has a north-south direction, the upper part of the reef will for at least part of the day cast a shadow over the lower living colonies and, by inhibiting the action of the zooxanthellae, and by retarding the growth of the coral, still further assist in the production of a vertical face." He agrees that " there appears to be some evidence of a definite connection between the intensity of the light falling on the coral-colony and the rate of its growth."

The direct effect of light on coral growth has been observed in a number of instances. Gardiner (1898) observed that in the clefts on the outer margin of Funafuti and similar atolls corals grew outwards from the walls of the fissures and then upwards, apparently the result of phototropism. Later (1903*a*) he speaks of the density of the skeleton decreasing with increasing depth. Wood-Jones (1912) states that " as a rule, coral zooids and coral colonies tend to grow upwards, and the general form of vegetative growth depends on this fact." The observations of Boschma and Verwey (1930) on *Echinopora lamellosa* are very illuminating. This coral normally forms horizontal plates, corallites being confined to the upper surface. Occasionally vertical plates are formed and then corallites appear on both surfaces. But stalked corallites may appear on the under surface of horizontal plates—in all cases apparently under conditions where some light can penetrate. If sufficient light penetrates then the stalks remain short, but in other cases, in regions where light is weak, the stalks elongate and grow outwards towards the margin of the colony. There seems no doubt that here we are dealing with a direct effect of light on coral growth. Kawaguti (1937*b*) has pointed out that corals living in feeble light have a more slender skeleton than colonies of the same species growing in regions of adequate illumination. He refers specifically to *Acropora palawensis* and *Halomitra robusta*. In a further paper (Kawaguti, 1937*c*) he describes experiments on regeneration and growth which reveal phototropism in all reef-builders which he examined.

Representatives of deep-water corals which occur amongst reef-builders are not affected by light. Referring to the Hydrocorallinae, Hickson (1924) points out that the Stylasterina, which have no zooxanthellae, extend from shallow water to the great depths. *Millepora*, on the other hand, which does possess zooxanthellae, has never been found below about 40 fathoms and does not flourish except near the surface. He further states that " the genus *Dendrophyllia* is one of the few reef-building corals which appears to be rarely found in water of less than 20 fathoms and to flourish in depths of 20–50 fathoms, and it is interesting that this genus is also one of the few corals that occur not only in the tropical seas but extend into the cooler waters of the Mediterranean Sea and Atlantic Ocean." But *Dendrophyllia* is *not* a true reef-builder. Like *Balanophyllia*, which has a similarly wide distribution, it has no zooxanthellae, and is to be regarded as a deep- and cold-water coral that has extended its vertical and horizontal distribution. Actually one species, *D. manni*, is abundant on the surface of reefs at Oahu, Hawaiian Islands, especially on the reef at Kanehoe Bay. Experiments by Edmondson (1928) revealed the significant fact that all planulae of this species settled in darkness, although only about 50% of the planulae of *Cyphastrea ocellina* did so. The latter lived for some three months, formed slight skeletal structure, but eventually grew paler and died. The former grew better; they eventually died but Edmondson attributes this to insufficient nutrition.

Thus, although the available data is not as extensive as could be desired, there *is* evidence that reef-building, but *not* deep-water, corals are influenced both in their manner, speed and solidity of growth by light. Phototropism of reef-builders, as recently emphasized by Gardiner (1936), certainly appears to be of prime importance in the formation of reefs, while the slowing down of growth in the absence of light and the formation there of weaker skeletons indicates a lowered metabolism. We know that under these conditions zooxanthellae are few or absent. The corals under these conditions are so sparse that lack of oxygen can hardly be the factor concerned, and there is thus reasonable ground for the tentative conclusion expressed at the end of the last section, namely, that in the absence of algae metabolism is depressed because waste products are no longer automatically removed.

7. REPRODUCTION AND DEVELOPMENT.

The settlement of planulae and development of young colonies in *Pocillopora bulbosa* and *Porites haddoni* has been described in beautiful detail by Stephenson (III, 3), who gives an adequate bibliography of previous work on development in corals. Abe (1937*a*) has since described post-larval development in *Fungia*. Details of later growth in relation to skeletal details of budding in *Pocillopora bulbosa* have been described by Manton (III, 6). Attention here will be confined to a consideration of breeding in relation to temperature—a matter which has an important bearing on the wider problem of distribution in reef-building corals.

The breeding temperatures of various Madreporaria were determined by Marshall and Stephenson (III, 8). *Favia doreyensis* spawned in the early summer when the surface temperature (as stated by Moorhouse; II, 4 (*b*)) was in the region of 30° C., and a species of *Lobophyllia* probably spawned about the same period. In a species of *Porites*, probably *P. haddoni*, breeding continued from January to May and, less actively, into July, although the absence of breeding throughout the rest of the year was not definitely determined. In *Pocillopora bulbosa* breeding was discontinuous, occurring about the time of new moon in the months December to April and about that of full moon during July and August (winter), with a transition period in May and June. Data were not obtained for the period from September to November, but it is possible that spawning occurs discontinuously throughout the year. A similar discontinuous spawning of *Maeandra areolata*, at the time of new moon in July and August, was observed by Yonge (1935*b*) at the Tortugas, while Abe (1937*a*) found a similar periodicity in *Fungia actiniformis* var. *palawensis* which planulates about the time of new moon from September to April at Palao. In neither case was the incidence of breeding studied throughout the entire year.

Examination of results on other reef invertebrates at Low Isles (Stephenson; III, 9) reveals that in respect of spawning species may be divided into four groups: (1) Those in which breeding is confined to a short period in mid-summer when the temperature is round about 30° C. (temperatures from Moorhouse; II, 4 (*b*)), *e.g.* in *Ophiothrix longipeda*, *Cypraea annulus* and *Hippopus hippopus*. The last named is included in the Tridacnidae (see Yonge; I, 11), and it is interesting to note that in the Red Sea the allied species, *Tridacna crocea*, also breeds at the hottest period in the year, namely, in early July, when the temperature approaches 30° C. (data kindly collected for the author by Dr. C. Crossland). (2) Those in which breeding is also extended into the spring and autumn, when the temperature exceeds about 24° C., *e.g. Acanthozostera gemmata*. This Loricate spawns throughout this period with lunar periodicity at the time of full moon. (3) Those in which breeding occurs in spring and autumn but *not* in summer, *e.g. Tripneustes gratilla* and *Pinctada margaritifera* (Nicholls, 1931). In the latter spawning occurred twice only, at the beginning of May and of November, in both cases when the temperature lay between 25° and 27° C. (4) Species in which breeding is continuous throughout the year, *e.g. Thalamita stimpsoni*, *Myrionema amboinense* and, possibly, *Trochus niloticus* (Moorhouse; III, 5).

Semper (1890) stated that in the Philippines periodicity of breeding in marine animals does not exist; he was able at all times of the year to find " fully grown specimens, young ones and freshly deposited eggs." Orton (1920) in his illuminating paper on sea-temperature and breeding in marine animals quotes this statement in support of his contention that, in the stenothermal conditions of tropical waters, reproductive periodicity does not occur. The work of the expedition reveals that in the waters around Low Isles, where the surface temperature in the anchorage varied between 20·25° and 33·0° C. (Moorhouse; II, 4 (*b*)), periodicity in breeding certainly *does* exist. This periodicity is clearly related to temperature, and is probably an important factor in controlling the distribution of tropical marine species, including corals.

Orton (1920) showed that, although individuals of a species may be capable of life within a wide range of temperature, they will only spawn between certain definite temperature limits. In Orton's words, " these temperatures appear to be physiological constants for the species." For instance the Portuguese oyster, *Gryphea angulata*, grows and flourishes when relaid in British waters but, because the temperature never attains the necessary minimum of 20° C., it never spawns. Nelson (1928) has listed the critical spawning temperatures for a variety of marine bivalves. The work of Runnström (1928, 1930, 1936) is of especial interest. He studied breeding temperatures in Norwegian waters and in the Mediterranean, and showed that the distribution of a species is controlled by the range of temperature within which it can spawn. For instance arctic-boreal species are animals which spawn between about -1 and 11° C. (true arctic species breed below 4·5° C. as shown by Thorson (1936)), boreal species those which spawn between 4° and 16° C. and mediterranean-boreal species those which spawn between 8° and 22° C. Species with a very wide distribution contain individuals capable of spawning at different temperatures in different regions. Runnström divided such species into two or even three physiological races. *Ciona intestinalis* he considers to be composed of a boreal race, breeding between 6° and 18° C., a mediterranean-boreal race, breeding between 8° and 23° C. and a mediterranean race breeding between 14° and 27° C. Animals with a still wider distribution, such as *Aurelia auritans*, he considers must comprise still more physiological races.

Other factors, such as the nature of the bottom, food, salinity, etc., being satisfactory, the horizontal distribution of any marine species probably depends on the temperature range within which it spawns. Species, in the words of Runnström, may be vegetatively eurythermal but are reproductively stenothermal. Considered from this standpoint the Barrier Reef invertebrates may be divided into the following provisional groups: (1) Mid-tropical species breeding about 30° C., *e.g. Favia doreyensis, Lobophyllia* sp. (?), *Ophiothrix longipeda, Cypraea annulus, Hippopus hippopus* and probably other Tridacnidae. These species will be confined to the mid-tropics or waters bounded by exceptionally hot land masses such as the Red Sea, where alone the surface temperatures attain this high figure. (2) Tropical species which breed between about 23° and 28° C., *e.g. Tripneustes gratilla* and *Pinctada margaritifera.* These resemble temperate species such as *Pecten opercularis* (Amirthalingam, 1928), which ceases breeding in the summer when the temperature exceeds 11° C. beginning again when it falls below this figure. (3) Species which, on Runnström's interpretation of the facts, may be composed of mid-tropical and tropical races, namely *Acanthozostera gemmata*, which breeds at all temperatures above about 24° C. (4) Species which have a still greater temperature range for spawning which occurs throughout the year at Low Isles, *i.e.* above 20° C. These include the corals *Pocillopora bulbosa* and *Porites haddoni*, and also *Myrionema amboinense, Thalamita stimpsoni* and possibly *Trochus niloticus.* These animals may, therefore, be composed of three physiological races, mid-tropical, tropical, and subtropical, the presence of the third permitting spawning between 20° and 24° C.

Other factors being suitable, therefore, the distribution of group (1) will be confined to the mid-tropics, of (2) to a more extended region throughout all waters within the tropics or with tropical temperatures, of (3) to the same region but without breeding in mid-summer, and of (4) to a somewhat wider area. An example is provided by the spawning of *Pinctada galtsoffi* at Pearl and Hermes Reef, an atoll near the western end of the Hawaiian archipelago (Galtsoff, 1933). Here the maximum water temperature is about 27° C. and this species breeds only once, in mid-summer, instead of twice, in spring and summer, as do related species in warmer waters, such as those of the Great Barrier (Nicholls, 1931).

The significance of this probably important factor in the distribution of reef-building corals has never been considered. Attention will be paid to it later when discussing the distribution of coral reefs.

8. GROWTH OF CORALS.

In the words of Gardiner (1931*b*), "the rate of growth of corals has fascinated every field naturalist recently working upon coral reefs. The extraordinarily luxuriant growth of the reef-building corals on the surface or in a few fathoms of water is before his eyes." It is unnecessary here to do more than refer very briefly to the results of the more important workers in this field. Gardiner himself (1898, 1903*a*) was amongst the first to provide adequate data for estimating the growth of Indo-Pacific corals. He found that in the Maldives the upward growth of young corals averaged some 25·6 mm. annually. Thus a reef 90 feet thick would be formed in 1000 years. Mayor (1924*c*) arrived at the very similar figure of 81 ft. in 1000 years as a result of work at Samoa. Wood-Jones (1907, 1912) made observations on growth at Cocos-Keeling and, while some of his conclusions have been criticized by Mayor (1924*c*), he established the fact that corals do not always grow steadily but usually by fits and starts. This has been confirmed by Mayor (1924*c*) and Stephenson and Stephenson (III, 7), while Tamura and Hada (1932) found great variation in growth rate amongst individuals of the same species. Boschma (1936) measured the increase in weight of a large series of corals from various areas around the Island of Edam in the Bay of Batavia. He found a percentage annual increase in weight varying between 16·9% for *Favia favus* to 1197·4 % for *Montipora ramosa*.

Vaughan (1911, 1913, 1915, 1916) made extensive observations on the growth-rate of Atlantic corals. He showed that the upward growth of *Orbicella annularis*, the principal builder in West Indian reefs, is from 5 to 7 mm. annually. This would produce a reef 150 ft. thick in 7620 years, taking the average rate of 6 mm. *Acropora palmata*, which grows more rapidly, would form a reef of similar thickness in only 1800 years. Edmondson (1929) found that at Hawaii, the northern extremity of coral distribution in the Pacific, corals grow less rapidly than in the mid-tropical Indo-Pacific, the rate corresponding more nearly to that recorded by Vaughan for West Indian corals.

The contribution of the Expedition to this aspect of the biology of coral reefs is contained in the valuable paper of Stephenson and Stephenson (III, 7). They found that, in a period somewhat exceeding six months, the branching forms (*Psammocora*, *Pocillopora*, *Acropora*, *Montipora*) added, on the average, from 33 to 95% to their original diameter. For massive corals belonging to the Astraeidae (*Favia*, *Coeloria*, *Lobophyllia*, *Symphyllia*, *Galaxea*) the average was lower, about 10%, but for massive forms of *Porites* some 17%. They also found evidence suggesting that, " if symmetry of a colony is interrupted by damage (in a branching form), the branches which are regenerated, or which grow out from neighbouring branches, to fill the gap, grow rapidly until symmetry is restored." This apparently innate tendency to form a symmetrical colony is further illustrated by the fact that in *Maeandra areolata* the form of the colony is identical, no matter whether one, two or three planulae (each of which gives rise to a distinct set of valleys in the adult skeleton) have gone to its formation (Yonge, 1935*b*).

The above figures are largely the outcome of observations made of experiments carried out in very shallow water. Verstelle (1932), however, made estimates of the rate of growth of corals *in situ* on various reefs in the Dutch East Indies. He found that growth was greater in depths exceeding 5 metres than it was between 3 and 5 metres, while above 3 metres it was usually much less. The maximum annual increase he found was 41·4 cm. (16·3 in.), while Sewell (1935) reports that a channel in the Andaman Islands shown to have a depth of 6 fathoms in a chart prepared in 1887 had only a depth of about a foot 37 years later. This gives an annual growth of almost 1 ft. While these are probably exceptional cases, Mayor (1924*c*) was very impressed with the vigour of coral growth several fathoms below the surface on the seaward side of reefs.

All workers in this field are agreed that young coral colonies grow more rapidly than larger ones and branching forms (in particular species of the great genus *Acropora*) more rapidly than solid forms. While it is true that the branches of the former are frequently broken off, these assist materially in reef formation because they are carried into interspaces between existing blocks, and, particularly near the surface, veneered over with a cementing layer of *Lithothamnion*. The sharp escarpment on the inner side of the shingle ramparts at Low Isles (see III, 2, plate xii, fig. 1) gives a clear indication of the manner in which these branched fragments interlock when carried on to the surface of the reef by wave action. Verstelle's figures in particular indicate that existing data on the growth rate of corals may represent minimum rather than maximum figures. Growth of corals near the surface is probably reduced owing to the great range of physical and chemical conditions.

9. MAINTENANCE OF REEFS.

The upward growth of reef-builders, the result largely of phototropism, leads to the eventual emergence of the summit of the reef above low tide mark.* The configuration of the reef is moulded by the action of prevailing weather. But reefs have to maintain themselves against the action of a variety of physical and biological factors. Of the former the most important is the erosive action of the seas which continually pound against their exposed slopes. This is usually more than counteracted by vigorous growth of coral, the reefs growing out against wind and weather. In the region where the surf breaks the reef crest is consolidated by the hard veneer of *Lithothamnion*. Although the actual amount of material supplied by these nullipores has probably been over-estimated, their importance, as a cement which binds together coral skeletons—whole or in fragments—shells, sand and the other constituents of the reef mass, cannot be overstressed. This was originally made clear by the observations of Gardiner (1898), and his recent work (1936) abundantly confirms these. Borings into coral reefs have revealed the unexpectedly loosely coherent nature of the coralline material below the surface (see Richards (1939) for an excellent survey of the results of borings on the Great Barrier and elsewhere). As a result of the growth of *Lithothamnion* such material is so consolidated that the surface of the reef crest when exposed at low spring tides often resembles a macadam road with a gentle slope seaward as shown in Plate V, fig. 8.

So long as heavy weather comes only from the prevalent source the reef is little damaged. Serious destruction comes only as a result of storms which beat against the lee. "Negroheads" or "niggerheads," massive coral boulders lying on the *leeward* surfaces of reefs, were a conspicuous feature of reefs around Low Isles, constituting the boulder zone. They were also common at the Capricorns in the far south, but absent in the Torres Strait. They are confined to the cyclone belt and probably represent the remains of mushroom-topped masses of coral which grew for long periods in the security of the lee of reefs before being thrown on to the reef surface as a result of cyclonic blows from northerly quarters during the summer. Umbgrove (1931) states that these boulders are of rare occurrence in the East Indies, which lie almost completely outside the cyclone belt. But many were thrown up by tidal waves produced by the eruptions of Krakatoa in 1883 and of Paloeweh in 1928; one of the former, which has a volume of 300 cubic metres, lies 100 metres from the shore near the lighthouse of Anjer. The devastating effect of the cyclone of 11th March, 1934, on the coral fauna and surface configuration of Low Isles has been described by Moorhouse (1936). It was fortunate that one of the members of the Expedition should have been present on the island when this cyclone hit it, and so was able to record changes in the original configuration mapped in such detail by Spender (1930).

The second physical factor which affects reefs is exposure to the air. This certainly

* Sewell (1935) and earlier workers quoted by him have expressed doubts as to whether, except in very shallow water, reefs can ever break the surface as a result of growth unaided by negative displacement of sea-level. They believe that nullipores, necessary for the cementation of the reef edge, cannot flourish at any depth. Sewell gives examples of submerged reefs which show no indication of upward growth. It is difficult to come to a definite conclusion on this matter. In protected waters there can be little doubt that reefs do rise unaided to the surface. A detailed study of conditions on these static submerged reefs, unfortunately an extremely difficult matter, seems the only way of solving this problem. Upwelling of cold water may be the explanation.

conditions the upward limit of coral growth and explains the flattened summits of reefs. Floods of fresh water may cause widespread destruction of inshore fringing reefs. Hedley (1925) described the destruction of the previously luxuriant fringing reef on the south-west corner of Stone Island, near Bowen, Queensland, during the cyclone of 1918. Between 22nd and 29th January, a total of 35·7 in. of rain fell at Bowen, and this coincided with full moon spring tides. In the words of Hedley, ". . . a thick layer of fresh water floated far out on the surface of the sea. When the low tide fell, this surface water sank till the whole reef was immersed in it. Then every living thing that dwelt there—corals, worms, shell-fish and crabs, died immediately. Putrefaction from these enlarged the zone of destruction. This slaughter reached as deep as 10 ft. below mean tide level." Crossland (1928*b*, 1939*a*) describes similar devastation of corals at Tahiti during exceptional rainfall in January, 1926. This involved later replacement of corals by *Lithothamnion* over large areas.

Occasionally corals are destroyed by more mysterious agencies. Wood-Jones (1912) refers to the destruction of all living coral in the south-east portion of the lagoon at Cocos-Keeling in 1876 following "the pouring out of foul water from a supposed volcanic vent at the southern side of the atoll." Thirty years later the tract of dead coral remained "on which the efforts at colonization has been practically unavailing." He ascribes this to the establishment of algae over the dead coral. Agassiz (1883) in his original description of the Tortugas reefs refers to extensive patches of *Madrepora*. Mayor (1924*a*) has described the later destruction of this species (actually *Acropora muricata*) by so-called "black-water," adding that "even yet (1922) this coral is rare or absent over the areas in which it was once the dominant form." In 1934 this species was certainly re-establishing itself, large colonies being observed by the writer in shallow water between Loggerhead Key and Fort Jefferson.

Biological agents of destruction consist of plant and animal organisms which bore into coral rock, and both by their own activities and by the assistance they give to the erosive action of the sea do extensive damage. They penetrate the rock usually mechanically but in some cases chemically, as in the various species of *Lithophaga*. Gardiner (1930*b*) was the first to lay especial stress on their importance as destructive agents, and later (1931) estimated that they may remove as much as 40% of the rock. The nature and action of the more important of these borers at Low Isles has been described by Otter (I, 12), and in the case of the burrowing species of *Tridacna* by Yonge (I, 11). Otter has combined the results of his own and Gardiner's observations on the subject in the form of a diagram illustrating the cycle of events in the destruction of a coral reef (I, 12 ; text-fig. 5). More recently Bertram (1936) has described the action of borers on the coral reefs of the Red Sea. He demonstrated the importance of boring algae in the undercutting of reefs of elevated coral rock. By softening the rock they render solution possible. On the other hand, his observations fail to confirm the opinion, previously expressed, that holothurians, which pass great quantities of sand through the gut, play any significant part in the further disintegration of sand into mud.

The mass of a reef at any time represents the balance between increase due to growth of the various reef-builders and loss due to the effects of physical and biological agencies. Mayor (1924*b*) has discussed the causes which produce stable conditions in the depth of the floors of Pacific fringing reef-flats. These have a uniform depth of rather less than 6 in. and this represents a balance between the same opposing forces. In Mayor's words, "the dead coral and limestone blocks which so thickly bestrew the reef-flat disintegrate rapidly, due largely to the activities of boring algae, while the living coral grows up to low-tide level and readily restores the loss. If, however, the growth of coral ever becomes so luxurious as to reduce the depth of the floor of the reef-flat to less than 6 in., the currents due to breakers and wind would become more rapid, and as everything alive or dead lies loosely about the reef-flat, the floor would become washed down to a balanced state of about 6 in. in depth. If, on the other hand, disintegration of material and poverty of coral growth caused the floor of the reef-flat to become deeper than 6 in., the current would decline in velocity and fragments washed in from the lithothamnion ridge would not be removed from the floor, so that new material would soon restore the depth to its balanced state of about 6 in."

In a series of papers on the coral reefs of Tahiti, Crossland (1928*a*, 1928*b*, 1931, 1939*a*) has advanced evidence in support of his contention that in this region, so far from growing seaward, the reefs are going back, in other words that the agents of destruction are greater than those of construction. His conclusions have been contested by Davis (1928), Sewell (1935) and Kuenen (1933). Reference should be made to these papers for the arguments advanced on both sides, but Crossland (1928*a*) raises the wider question as to whether the present age of corals is not passing and the conditions he has claimed to prevail at Tahiti are not world-wide. He produces in support of this his earlier observations at Zanzibar (Crossland, 1902) and also those of Fryer at Aldabra (well summarized by Gardiner, 1931*b*) and by Mayor in a certain area off Samoa. Gardiner (1936) produces evidence of a widespread regression of coral reefs in the south-west Indian Ocean, and accounts for this by the absence in this region of a protective veneer of nullipores. But observations on the reefs of the Great Barrier, from regions as far apart as Mer Island in the far north, the region from Cook's Passage to Trinity Opening in the centre, and the Capricorn Islands in the south, all indicated the great virility of the marine communities which formed these reefs. The same conclusion is implicit in the writings of Boschma, Umbgrove, Verwey and Kuenen on the reefs of the Dutch East Indies, while, as noted above, Sewell's observations in the central region of the Indian Ocean lead him to the same result. Whatever the cause for the regression of reefs in the more outlying regions of the Pacific and Indian Oceans, it does certainly not appear to be of universal occurrence.

10. THE FORM OF CORAL REEFS.

The symmetry of coral reefs which has been stressed in this paper, especially in connection with the resultant environments for coral growth, is the outcome of the interactions of two factors—the action of the prevailing currents and the outward growth of corals in the direction of these currents. The importance of these factors is implicit, if not always explicit, in the writings of the many students of coral reefs. The facts have been well reviewed by Vaughan (1919*a*, 1919*b*). Their effect in its simplest form is admirably displayed in the configuration of the fringing reef which surrounds Mer Island in the Torres Strait. The long axis of this volcanic island lies almost at right angles to the currents produced by the trade winds. On the windward side the reef is from 1800 to 2200 ft. wide, with an impressive lithothamnion-covered reef crest, in the shelter of which lies an area of shallow water in which branching corals, notably *Seriatopora hystrix*, are abundant. On the lee shore of the island, off the sand dunes which collect in the still water, the reef is only 175 ft. wide and about half of this is composed of sandy beach (see maps in Mayor (1918*a*) and Yonge (1930)). Where reefs fringe a continental land mass they grow seawards, enclosing a shallow lagoon channel, but sandy areas are largely absent. Vaughan (1919*a*) and others postulate submergence as an essential factor in the formation of a fringing reef, but, assuming the presence of a suitable bottom, it appears possible for this type of reef to grow outwards against the action of the surf for a considerable distance in the absence of earth movements.

The effect of the Pacific surf, driven by the south-east trade winds, is clearly shown in the form of the Outer Barrier reefs as originally described by Paradice (1925) and in fuller detail by the Shore Party of the Expedition (III, 2). The centre of the reef grows out against the current while its margins are curled back by the action of this, which carries sand and debris into the still water in the lee. The diagram of Yonge Reef (III, 2, text-fig. 5) should be consulted in this connection.

As emphasized by Vaughan (1919*a*) and Gardiner (1931*b*), atoll-like formations can be divided into two groups. There are small formations, designated *faros* by Gardiner (1903*a*), which arise on extensive shallow platforms, and larger formations, true atolls, which frequently occur in mid-ocean and whose margins are co-extensive with those of the submarine elevations on which they have arisen. The former occur particularly in the Maldives, being described by Gardiner (1903*a*), in the Florida reef area, in the channel between the northern half of the Great Barrier and the mainland and in the Malay Archipelago. Low Isles is a typical example of such a reef. These reefs are certainly moulded in form by the action of prevailing wind-generated currents. Their probable mode of origin was originally outlined by Hedley and Taylor (1907), who give a diagram indicating how a linear reef lying across the path of prevailing currents will be converted into a crescent. The maps prepared of Low Isles and of Three Isles (III, 2, pls. i, ii) reveal a concave reef with the convexity pointing south-east and a shallow anchorage with a rounded sand key in the lee. The subsequent evolution of these reefs, involving negative displacement of sea-level, the consequent formation of shingle ramparts and the establishment in the shelter of these of mangrove swamps and, in the lee, of the sand cay fringed and buttressed by flattened expanses of beach rock, is outside the scope of this paper. Full details are given in the papers of the Geographical members of the Expedition (Steers; III, 1, 1929, 1937, 1938; Spender, 1930). Evidence of widespread lowering of sea-level, first stressed by Gardiner (1898, 1903*a*), has been well reviewed by Sewell (1935). The presence of raised platforms along the Queensland coast, described by Steers and also observed by the author at East Strait Island and elsewhere in the Torres Strait, indicates a total negative displacement of sea-level of 18 to 23 ft. in this region. The absence of islands on the Outer Barrier reefs may be explained by the greater force of the sea, which never permitted the establishment of the essential preliminary rampart.

The Tortugas and Marquesas Keys in the Gulf of Mexico are essentially similar. In the former, the origin of which has been outlined by Vaughan (1914), the reef complex is much larger, with wide stretches of water between the islands and reefs exposed at low tide. But on the exposed north-east side at Long Reef are shingle ramparts and even, in their lee, occasional mangroves, while the large sandy island of Loggerhead Key lies in the lee. The influence of water movements on the configuration of banks of this character is most strikingly displayed by the Marquesas Keys. As shown by Vaughan (1914), there are here no important coral growths, the foundation being possibly oolite, while the keys themselves are composed of calcareous detritus with *Halimeda* as the most important constituent. Yet the keys are arranged in a circle enclosing a shallow lagoon. Currents alone are responsible for this formation.

The effect of prevailing wind-generated currents on the geomorphology of reefs is again admirably shown in many of the coral formations of the East Indies. Umbgrove (1928, 1929*a*, 1929*b*) has described the effect of the northerly monsoons on the reefs in the Bay of Batavia and of the easterly monsoons on those of the Thousand Islands in the Java Sea. The effect is essentially similar to that later described by the Geographical members of the Expedition for Low Isles and similar reefs. On the other hand, more recently Umbgrove (1929*b*) has shown that the reefs of the Togian Islands in the Gulf of the Tomini in northern Celebes, where winds are not constant over long periods, show "no single trace of the action of wind or waves." Both Verwey (1931*b*) and Kuenen (1933) have confirmed and extended these findings.

The effect of currents on true atolls is more debatable. Wood-Jones (1912) considered that the form of Cocos-Keeling atoll was due entirely to the action of currents, and illustrated his views with a series of diagrams. Krempf (1927) believed that atolls in Indo-China were moulded by the action of currents created by the alternating monsoons. But the great size of many atolls, their co-extension with the submarine platforms and the depth of their lagoons combine to render such an explanation of their form unlikely. As Gardiner (1930*b*) has shown, the problem of atolls is contained in the problem of the formation of their lagoons. While currents must have played a part in the configuration of atolls, in this case the growth of corals appears of greater importance. In the absence of shallow water in the lee where sand can collect and turbidity be produced, outward growth of corals is presumably possible in all directions. The manner of lagoon formation leads beyond the scope of this paper and the experience of the author. Gardiner (1903*a*, 1930*b*) is convinced that they have been excavated, and the greatest respect is due to opinions backed by Gardiner's wide personal knowledge of atolls. Vaughan (1919*a*), on the other hand, believes that lagoons are too deep ever to have been excavated by solution or any other destructive agency. This implies that a solid reef mass was never antecedent to an atoll, but that the ring grew up *in situ*, as Krempf (1927), largely on the analogy of the formation of micro-atolls, believes to be the case. This seems possible only if the reefs were formed early during the course of geologically recent submergence, which Vaughan actually postulates. This might well produce conditions of turbidity, etc., in the centre of the platform which would inhibit significant growth of corals except round the periphery. Certainly in fully-formed lagoons the muddy nature of the bottom (although not universal, as stated by Gardiner (1931*b*) and Sewell (1935)), the presence in this of sulphuretted hydrogen (Sewell, 1936), the turbidity of the water aided by the amorphous deposits of calcium carbonate described by Gardiner (1931*a*, 1931*b*) will inhibit coral growth which is certainly conspicuous by its absence (Gardiner, 1936). Kuenen (1933), in a comprehensive review of the problem of atoll formation, concludes that atolls "are essentially the products of reef growth combined with a sinking substratum." Atoll formation remains as the supreme problem confronting workers on coral reefs.

11. DISTRIBUTION OF REEF-BUILDING CORALS.

Much of what has been related in the foregoing sections may conveniently be discussed in relation to the distribution, both horizontal and vertical, of reef-building corals. Vaughan (1931) summarizes the conditions necessary for vigorous growth of reef-building corals as follows: "(*a*) Depth of water, maximum, about 45 metres (25 fathoms); (*b*) bottom firm or rocky, without silty deposits; (*c*) water circulating, at times strongly agitated; (*d*) an abundant supply of small animal plankton; (*e*) strong light; (*f*) temperature—annual minimum not below 18° C., minimum average temperature for the coldest month in the year not lower than about 22° C.; (*g*) salinity between about 27 and about 38 parts per thousand." The only criticism to be made on the above concerns (*b*), the presence of coral islands in the Bay of Batavia showing that reefs can arise from a muddy bottom.

Coral reefs are confined to the tropics with the major exceptions of those of Bermuda and of the Red Sea, and almost exclusively to the middle and western areas of the oceans. Darwin and Dana both realized that horizontal distribution was controlled primarily by temperature. The coral fauna of the Atlantic is much poorer than that of the Indo-Pacific and is quite distinct from it; even where the same genera occur in both regions, *e.g.* *Porites*, *Acropora* and *Favia*, the species are not closely related (Vaughan; 1919*a*, 1919*b*). The older Tertiary coral fauna of the West Indies is much richer in species, but at this period the Pacific and Atlantic were connected across Central America. According to Vaughan (1919*b*) in middle and later Miocene times the two became separated, and "by Pliocene time the corals of distinctive Indo-Pacific facies had become extinct on the Atlantic side, so that the Pliocene coral fauna of Florida is purely Atlantic in its affinities. After the differentiation of the Atlantic from the Indo-Pacific fauna it seems that there was a short connection somewhere that permitted the Atlantic fauna to extend on the Pacific side of America up to the head of the Gulf of California."

The extension of coral reefs beyond the tropics is due to local hydrographic conditions, in the case of Bermuda to the influence of the warm waters of the Gulf Stream which flow between these islands and the mainland of America, and in that of the Red Sea to the effect of the adjacent hot land masses. The absence of reefs on the eastern sides of the oceans is certainly due in large measure to cold currents and upwelling of cold water along the western shores of the continents. The surface isotherms converge to such an extent that the possible distribution of reef-builders on the west coast of Africa extends only within the Gulf of Guinea and on that of America only between southern California and the Galapagos. Thiel (1928) has given the most detailed account of Madreporaria from the former region. He lists 29 species but the majority occur only on the islands, the coastal fauna being restricted largely to species, such as those of *Caryophyllia* and *Dendrophyllia*, found in colder seas. Many of these species are migrants from the Indian Ocean which have spread up the west coast of Africa from the Cape of Good Hope. Thiel attributes the great paucity of true reef-builders on this coast to the low temperature of the water; such reef-builders as do occur on the islands, where the water is somewhat warmer, never grow with sufficient vigour to form reefs.

While no such barrier of temperature would appear to prevent the construction of reefs along the western shores of central America, there is a striking diminution of species of reef-builders from west to east in the Pacific. This is apparently due to the westerly set of the currents. The East Indies are usually regarded as the focus of coral growth and evolution (Gardiner, 1931*b*), and in the Indian Ocean the fluctuating currents permit of wide distribution of pelagic larvae. Gardiner (1931*b*) points out that "over the whole area of the Indian Ocean the reef-builders—and the large majority of other forms of life associated with them—are identical. There are the same genera and about the same number of their species in the Maldives, Chagos and Seychelles, these being the same species as on the surrounding continental shores." Thus Vaughan (1918*a*) describes 20 genera of Madreporaria from Cocos Keeling in the eastern side of the Indian Ocean, and Crossland (1935, 1939*b*) mentions 24 genera as occurring in the Red Sea. It is otherwise in the Pacific. In terms of genera (including *Tubipora* and *Heliopora* ; also *Millepora*), Eguchi (1938) lists 48 from Palao in the Western Pacific, Umbgrove (1939*a*) 41 from the Bay of Batavia, Vaughan (1918*a*) 29 from Mer Island (which to the author's personal knowledge should be increased to *at least* 41 for the Great Barrier generally) ; in the west central Pacific Hoffmeister (1925) lists 29 genera from Samoa and Fiji ; in the central Pacific Crossland (1928*b*, 1939*a*) mentions 14 genera, 5 of which are in process of disappearance while 16 important Indo-Pacific genera are absent ; in the Marquesas, where no reefs are formed, Crossland (1927) found only 7 genera, while at Panama, where Crossland (1927) observes that the littoral fauna is of exceptional richness, he found only 5 genera of corals. No reefs were formed by them either here or at the Galapagos where apparently the coral fauna was no richer.

There seems no good reason for abandoning the view that it is temperature which controls the horizontal distribution of reef-building corals, merely qualifying this by reference to the probable effect of currents in the distribution of the planulae larvae. It should also be borne in mind, as stated in the section dealing with reproduction, that temperature may exert its effect *primarily on reproduction* and not on the individual. But mention must be made of the suggestion put forward by Hardy and Gunther (1935). In their hypothesis of "animal exclusion" they state that phytoplankton create an uncongenial environment for animal life, and that Foraminifera, Radiolaria and also corals which live near the surface waters and contain symbiotic algae have been able to overcome the excluding influence by "some counteracting physiological process." In the development of this theory they state that passage from polar, by way of temperate, to subtropical and tropical seas involves passage from "regions of high nutritive salt content and rich 'free' phytoplankton with apparent exclusion effects to regions of very low nutritive salt content and 'imprisoned'* (symbiotic) phytoplankton without the effects of the exclusion of the animal plankton from the sunlit surface layers." This leads them to the suggestion that the distribution of coral reefs "may be associated with water masses which by currents have travelled farthest from the predominantly 'free' phytoplankton regions, or perhaps more reasonably that they occur in water in which the 'free' phytoplankton never or only rarely reaches a concentration sufficiently high to bring about exclusion effects." The value of this suggestion depends in the first place on the validity of the hypothesis of animal exclusion. Space does not permit of a discussion on this matter, but it may be noted that not less potent arguments are advanced by those who believe that phytoplankton is controlled by the "grazing" activities of the zooplankton, *e.g.* by Harvey, Cooper, Lebour and Russell (1934) and, most recently, by Flemming (1939). The prevalence

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* The description of zooxanthellae as "imprisoned" phytoplankton was originally made by Yonge (1931).

of "imprisoned" phytoplankton in tropical as compared with temperate and polar seas is certainly very striking. But it is equally certainly one of the causes and only very questionably one of the *results* of the limited quantities of nutritive salts. Hardy and Gunther suggest that if this phytoplankton were not so imprisoned its presence would "exclude" that of the corals (whether by a direct effect on these or by way of its effect on the zooplankton is not made clear). There is no evidence that such would be the case. The prevalence of symbiotic algae within the tissues of tropical marine invertebrates may, in the present state of knowledge, be explained from the standpoint of the algae as a result of the greater nitrogen—and also phosphorus—"hunger" (to quote the old but illuminating phrase of Brandt), and from that of the animals as of survival value in evolution in view of the increased metabolic efficiency it confers in some cases (*e.g.* Madreporaria) and increased food supply in other (*e.g.* Tridacnidae).

Distribution in depth of reef-builders is a problem of no less importance. Darwin (1889) came to the conclusion that "in ordinary cases reef-building polypifers do not flourish at greater depths than between 20 and 30 fathoms." Dana (1890) gives 20 fathoms as the ordinary depth to which they extend. More recent workers have not significantly modified these figures beyond, as already pointed out, indicating the correlation between turbidity and vertical distribution. There is little doubt that a depth of some 25 fathoms does represent the maximum vertical range of reef-builders. In this case temperature cannot be the controlling factor. Dana realized this, pointing out that the temperature at the 100-foot plane in the middle Pacific is above that necessary for the existence of reef-builders. Mayor (1924*a*) found that off the seaward edges of the reefs at Tutuila, Samoa, there was usually less than a degree difference in temperature between the surface and depths of 200 ft. Off the seaward slopes of the Great Barrier Reef there was negligible change in temperature between the surface and 50 metres, but between that depth and 100 metres "there was a rapid fall in temperature which continued to the greatest depth sampled (600 metres)" (Orr; II, 3). But the average difference in temperature between the surface and 100 metres was only 3·4° C.

It is becoming increasingly clear that light is the factor controlling the vertical distribution of corals. The evidence for this was summarized in section 6 of this paper. Coral growth appears to be most intense some little distance below the surface. Gardiner (1903*a*) says that it reaches maximum luxuriance from 3 to 6 fathoms below the surface while, as already noted, Verstelle (1932) found that corals grow more rapidly below 5 metres than in shallower water. Mayor (1924*c*), as a result of observations made with the aid of a diving-hood off the seaward edge of Aua Reef, Samoa, states that "in the pure ocean-water, at depths of 1 to 6 fathoms under the breakers, the corals grow with a vigour unseen elsewhere. The individual stocks are many times larger than those of the same species growing in the shallow water on top of the reef-flat. Stocks of *Acropora hyacinthus* 3 ft. in diameter are common, as are also branching *Acropora* covering 25 sq. ft. in area. About three-quarters of the area of the seaward slope down to 4 to 6 fathoms off the Aua Reef is completely covered with coral-heads. The stems and stocks of these corals are stouter and of stronger build than those of corresponding species growing in the relatively quiet water of the shallows on top of the reef-flat." Edmondson (1929) states that at Hawaii, where corals are sparse on the reef surface, "they show much greater activity on the outer rim, at depths of from 2 to 4 fathoms." Verwey (1931*b*) describes the vigour of coral growth below a depth of 5 metres on the seaward side of reefs.

If corals are affected by light, by its effect on their contained zooxanthellae, we might expect some indication of optimum conditions for the activity of the latter in water of moderate depths. Unfortunately experimental work has of necessity been confined to sheltered waters on the lee of reefs where turbidity is higher and light penetration correspondingly less than on the seaward slopes. Yet the results of experiments on photosynthesis in zooxanthellae (Yonge, Yonge and Nicholls: I, 8) did indicate that, above some critical degree of illumination, reef-building corals contain the maximum content of zooxanthellae. An experiment was carried out in which corals were exposed for similar periods at varying depths on successive days. The results showed a progressive diminution in oxygen content at successively greater depths. But these experiments were carried out in midwinter (11th–17th July, 1929), when light penetration would be at its minimum and temperature at its lowest. Similar experiments were later carried out at the Tortugas in the summer of 1934. Unfortunately the unusually broken weather which prevailed that season impaired the value of the results, which consequently have not been published. In one case, that of *Porites asteroides*, there was actually greater oxygen production at 8 metres than at the surface, while in another, that of *Orbicella cavernosa*, there was greater photosynthesis at 4 metres. But only experiments carried out in the clear water on the seaward side of reefs would answer this question. It is worth noting that Riley (1938) found that phytoplankton at the Tortugas showed maximum photosynthesis at depths of between 10 and 15 metres. It has to be remembered, however, that the zooxanthellae are to some extent screened by the tissues of the coral in which they live.

The view that light is the dominant influence in the vertical distribution of reef-builders and the major factor controlling speed of growth would certainly provide an explanation for the growth of reefs against prevailing currents. This has usually been attributed to the greater content of plankton in the water on the seaward slopes and to its greater oxygenation. There is no evidence that the former is the case and the reverse may actually be true—there was certainly more plankton in the channel within the Great Barrier reefs than in the open Pacific outside (Marshall: II, 5). Oxygenation may have some effect, but it is certainly true that light penetration is much greater in these clearer waters. Outside the Barrier Secchi disc readings as high as 40 metres were obtained, whereas within the lagoon channel near Low Isles average visibility was about 12 metres (Orr: II, 3). It is not unreasonable to assume that the vigour of coral growth on seaward slopes of reefs, so graphically described by Mayor (1924*c*) and Verwey (1931*b*), is due to the greater penetration of light here, with consequent effects on the metabolism of the corals by way of the zooxanthellae and possibly also directly.

The deep and cold-water coral fauna differs from the reef-builders in the absence of zooxanthellae. It is composed partly of solitary corals, such as attached *Balanophyllia* and *Caryophyllia* or *Flabellum* which lives free on a soft bottom, young individuals only being attached (Gardiner, 1929). There are also delicately branching forms such as *Lophohelia*, which forms relatively extensive banks on hard bottoms in the Norwegian fjords (Nordgard, 1929), and *Dendrophyllia*, which has been referred to frequently in the course of this paper. But in addition there is in the tropics an intermediate coral fauna found at depths of between 46 and 74 metres and, mixed with true deep-water species, as deep as 183 metres (Vaughan, 1919*b*). This was first recognized by Gardiner (1903*a*), and its possible importance as a basis for the later establishment of reef-builders emphasized. Vaughan (1907) gave a detailed account of this fauna in his work on the corals of the Hawaiian Islands and Laysan. He states that a temperature of about 22·8° C. marks the boundary between shoal-water corals and those of intermediate depths, which are in turn bounded by a minimum temperature of about 15·6° C. The various species of deep-water genera have a wide temperature range, extending from −1·12° C. in the abyssal seas to the temperatures of tropical reefs on which species of *Dendrophyllia* are common.

12. EVOLUTION OF REEF-BUILDING CORALS.

Certain views on evolution in reef-building corals are implied in this paper. It has been claimed that many of the adaptations of these animals have arisen since reefs rose to the surface of the sea, thereby bringing into existence the various environments for which different species of corals are certainly now adapted. It seems needful, therefore, to conclude with a few words on this subject.

Possibly attached cup-corals such as *Carophyllia* and *Balanophyllia* (imperforate and perforate respectively) represent the nearest approach to the primitive form amongst existing corals. They are essentially actiniarians with the power of secreting by means of the ectoderm a skeleton consisting of basal disc, surrounding theca and inwardly radiating septa. It may further be assumed that these animals evolved originally in shallow water. Gardiner (1939*b*) states with reference to deep-water corals that " all modern reports on corals and many other marine animals are based on a supposition of gradual migration from shallow to deep seas." No one will dispute this statement as far as the deep-water corals are concerned, but one of the theses of this paper is that, in addition, the modern reef-builders migrated upwards and, in the course of time, evolved many genera and species adapted for life in the various regions on the reefs and also in connection with life between tide-marks.

Formation of colonies by corals may further be assumed to be secondary. Palaeontological evidence indicates that the astraeid corals are the most primitive of these (Zittel, 1927), and it is noteworthy that these large-polyped corals with massive skeletons are derived most easily from cup-corals and would, unaided, be capable of forming reefs. Branching corals, such as the Stylophoridae, Pocilloporidae, Oculinidae and Acroporidae evolved more recently, the Acroporidae apparently last of all. They are the most vigorous of all reef-builders and their evolution may well coincide with the full development of modern coral reefs. The Fungidae (and Agaracidae) amongst reef-corals and the Turbinolidae amongst deep-water corals are also more recent that the astraeids. The appearance of the Fungidae may be associated with the development of sandy areas in the lee of reefs. Possibly *Maeandra areolata* evolved from the parent maeandrine stock at about the same period, certainly in connection with the same habitat. The Turbinolidae are similarly adapted for life in the mud of deep seas (see Gardiner, 1939*a*). The Agaricidae, amongst the most specialized of all modern corals, are in many cases animals of the shore zone, with small polyps, often with encrusting growth and frequently relying on water movements to assist in cleansing, while many of their species are highly adapted physiologically for shore life.

Restrictions of space make it impossible to develop this theme further, but it is suggested that the adoption of this viewpoint may be of assistance to palaeontologists and others interested in the evolution of modern corals.

13. SUMMARY.

1. Coral reefs are marine communities occurring in shallow waters within the tropics, the dominant organisms being Madreporaria containing zooxanthellae (*i.e.* reef-building corals).

2. The upward growth of reef-builders has led to the formation of reefs, the height of which is limited by the effect of exposure to the air while their general form is moulded by the action of prevailing, usually wind-generated, currents.

3. Many species of reef-builders have become adapted morphologically and physiologically for life between tide-marks. Different genera and species of corals are also adapted for life in the diverse environments between the seaward and sheltered sides of reefs. An initial capacity for reef-building has raised problems of existence which subsequent adaptation has solved.

4. Corals are specialized carnivores feeding on zooplankton for the capture and digestion of which they are highly specialized.

5. Certain species are highly adapted for life in a particular environment, while other corals are capable of wide modification in form which enables them to live in a variety of environments.

6. Reef-builders are capable of removing, by means of cilia on the coenosteum, relatively large quantities of falling sediment.

7. Unattached corals which live free on a sandy bottom can uncover themselves when buried. Only certain species which live always in the surf region rely entirely on water movements for cleansing.

8. Species which live between tide-marks are adapted physiologically for resisting extremes of temperature and salinity and the effects of exposure to the air.

9. Association between corals and zooxanthellae is essential to the zooxanthellae which never occur free in the sea. It is not essential to the life of *individual* coral colonies.

10. The zooxanthellae play no part in nutrition of the corals. The significance to the corals of the oxygen produced by the algae during photosynthesis is uncertain. The zooxanthellae certainly act as organs of excretion, automatically removing waste products of coral metabolism. By so increasing the metabolic rate of the corals they may be an indispensable factor in the necessarily exceptional powers of skeleton formation possessed by the marine *communities* known as coral reefs.

11. Evidence on the effect of light on coral growth is discussed. Reef-builders certainly exhibit phototropism, and there is evidence that they are also influenced by light in both speed and solidity of growth.

12. Data on the breeding temperatures of reef-builders and other reef invertebrates is analysed and the conclusion reached that, other factors being satisfactory, the horizontal distribution of reef-builders probably depends in the first place on the temperature range within which they can spawn.

13. Examination of data on the growth of corals reveals that this is greatest about 5 metres below the surface.

14. Reefs are continually being destroyed by physical and biological agencies, and

the mass of a reef at any time represents the balance between increase due to growth and loss due to these agencies.

15. The asymmetry of coral reefs is the outcome of the interactions of two factors—the action of prevailing currents and the outward growth of corals in the direction of these currents. The formation of islands on their summits is probably normally only possible after negative displacement of sea-level.

16. The horizontal distribution of reef-builders is controlled by temperature and, within waters warm enough for their existence, by the nature of the bottom and the direction of the currents which carry the planulae.

17. The vertical distribution of reef-builders appears to be controlled primarily by light, acting possibly both directly on the corals and by way of its effect on the zooxanthellae.

18. It is suggested that many of the existing reef-builders evolved after reefs had grown upwards and brought into being, on their seaward and sheltered slopes and on their summits, the various environments for life in which these corals are now adapted.

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APPENDIX

A NOTE ON THE APPEARANCE OF LIVING CORAL POLYPS.

(BY PROF. T. A. STEPHENSON.)

The appearance of living Madreporarian polyps, in good health, is less extensively known than that of the related sea anemones, and they have been less fully illustrated in the literature. Drawings of living polyps exist in a number of works, but these, with notable exceptions and especially in the older publications, are apt to be somewhat wooden if not imaginative, and to give little idea of the real appearance of the polyps portrayed. On the other hand several excellent photographs of living polyps exist, though these are relatively few in number. In the reports of the present series new photographs have been published, showing the appearance in life of polyps belonging to species of *Goniopora* (Vol. I, no. 2, Pl. II, fig. 6; and Vol. I, no. 2, Pl. I, fig. 1, accidentally named *Favia*), *Lobophyllia* (Vol. I, no. 2, Pl. I, fig. 2), *Fungia* (Vol. I, no. 2, Pl. I, fig. 4), *Montipora* (Vol. III, no. 2, Pl. X, fig. 3) and *Euphyllia* (Vol. III, no. 8, Pl. I, fig. 1).

One of the most noticeable features of a coral reef is the fact that if it is visited by daylight the majority of the corals have their polyps contracted with the tentacles hidden.

So far as my own experience in Australia is concerned, this applies to species of *Acanthastrea*, *Acropora*, *Astreopora*, *Coeloria*, *Cyphastrea*, *Echinopora*, *Favia*, *Favites*, *Fungia*, *Goniastrea*, *Herpetolitha*, *Hydnophora*, *Leptastrea*, *Lobophyllia*, *Merulina*, *Montipora*, *Pachyseris*, *Pavona*, *Platygyra*, *Porites*, *Psammocora*, *Seriatopora*, *Stylophora*, *Symphyllia* and *Tridacophyllia*. There are, however, exceptions, some of which are mentioned in the following list:

Acropora. Colonies belonging to certain species of this genus may sometimes be seen with partially extended tentacles during the day, but the majority of the species expand only at night.

Dendrophyllia nigresans and other species of corals dredged from deep water will frequently expand their polyps in captivity, at least in a weak light.

Euphyllia glabrescens (and perhaps other species of the same genus). Colonies were seen, both in pools on the reef and in deeper water when diving, with the tentacles well expanded in daylight (Vol. III, no. 8, Pl. I, fig. 1), and sometimes with commensal prawns among the tentacles. (*N.B.*: The polyp of this species is apparently incapable of complete contraction. C.M.Y.).

Fungia. In this genus some of the species expand properly only at night (*e.g. F. danai*), whereas others (*e.g. F. actiniformis*, Vol. I, no. 2, Pl. I, fig. 4) extend their large tentacles fully during daylight, on the reef as well as in aquaria.

Galaxea fascicularis commonly has the tentacles partly extended in the daytime, on the reef.

Goniopora tenuidens normally has the polyps extended to a considerable length in daylight, on the reef.

Hydnophora. C. M. Yonge has frequently seen colonies of *H. exesa* expanded in the daytime.

Montipora ramosa and *Pocillopora bulbosa*. In these species the habit is variable. Sometimes the polyps are well expanded during the day, in shallow pools on the reef; in other cases entirely contracted.

Porites. Massive species of this genus sometimes expand in daylight, especially towards evening.

Turbinaria. A colony belonging to this genus was kept in captivity for several days, the polyps expanding readily in daylight (Plate I). This was sometimes observed on the reef also, but in other cases the polyps showed no tendency to expand in daylight.

This list does not exhaust the exceptions, but in spite of their existence, the generalization already made holds good, namely that on the whole a daytime visit to the reef reveals relatively few expanded polyps. At night, however, a very different picture is presented. Many colonies are then covered by a forest of extended tentacles, which often form a transparent diaphanous mantle over the whole colony. These tentacles often almost colourless, in other cases showing gleams of suffusions of colour, in yet others being opaque or positively coloured. The bright colours of many colonies reside chiefly in the oral discs and columns of the polyps; in other cases in the tentacles also. The tentacles are often long in proportion to the size of their polyps, and have a considerable reach. In the photographs reproduced in Plate II a typical "night-flowering" coral is shown (a species of *Favia*). In the upper figure the appearance of the colony during daylight may be seen. Each polyp (usually with one mouth, sometimes with two or three) has a brilliant iridescent green oral disc (pale in the photograph) and a chestnut-brown column, which completely hides the tentacles during the day. In the lower figure the appearance of the same colony at night is seen (photographed by flashlight), the white tentacles being fully displayed.

It may further be noted that the general coloration of living coral colonies, due to the polyps and the tissues between them, is very distinct, even when the polyps are contracted during daylight. The commonest colours for whole colonies contrary to general belief are various yellowish and brownish shades. This does not mean, however, that brighter colours are uncommon, and these include pure deep violet, vivid greens, delicate blues, magenta and various other shades. A great deal of the beauty of living coral is derived from the fact that the delicate texture of the skeleton is often visible through the contracted flesh ; and this may be enhanced by a change of colour, in branching forms, from the main bulk of the branch to the tip. Thus, in the genus *Acropora*, the branches may be buff with lilac-blue tips, deep green with violet tips, pale brown with golden tips, or may display some other such combination. The commensal fishes which often frequent the colonies add still more to the effect, as when a reddish-brown colony has thirty or forty small brilliant yellow fishes swimming among its branches.

DESCRIPTION OF PLATE I.

FIG. 1. Part of a colony of a species of *Turbinaria*, with its polyps expanded, in the daylight. About natural size.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.). REPORTS, VOL. I. No. 13. PLATE I.

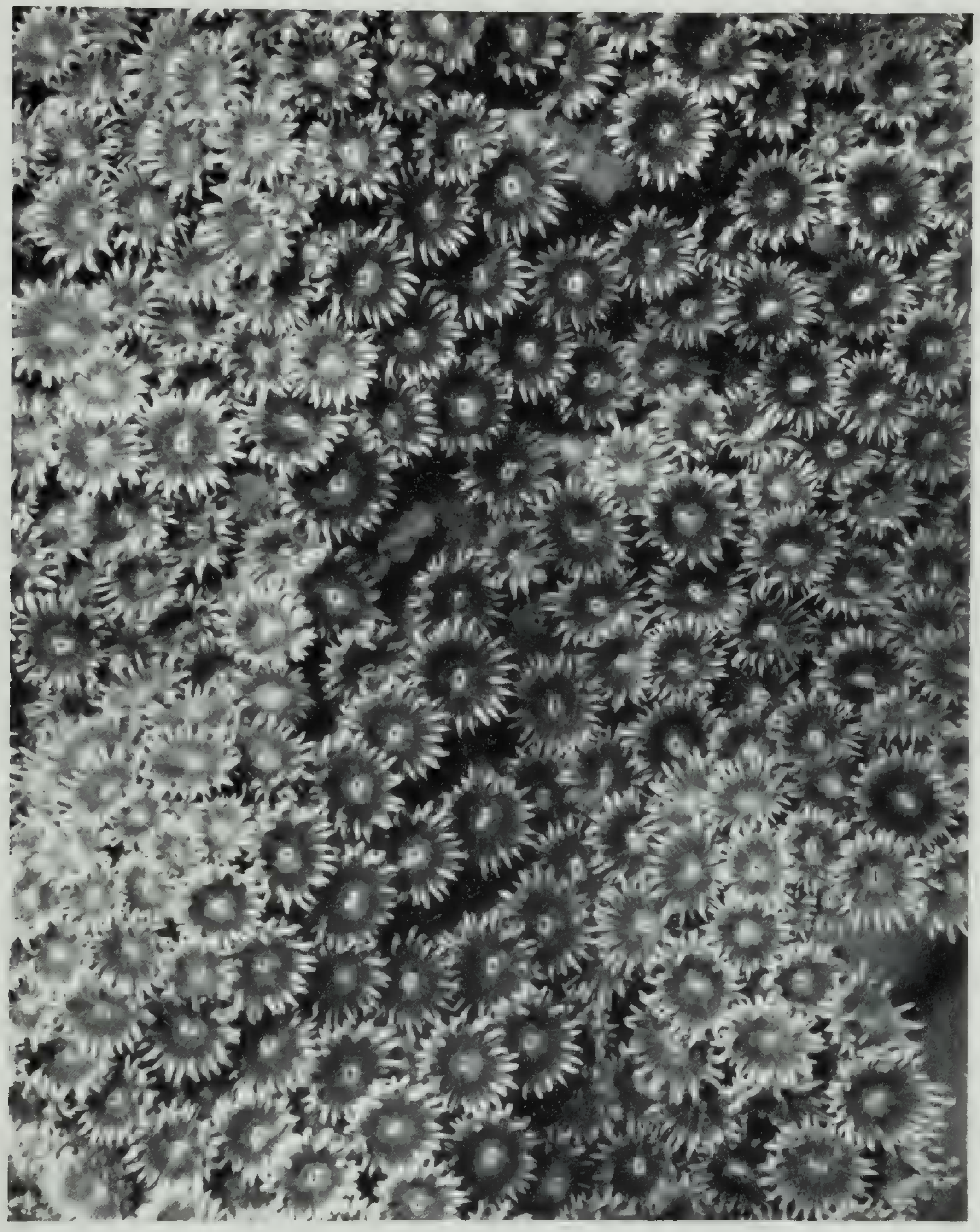

FIG. 1.

Photo T. A. Stephenson.] [*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE II.

FIG. 2. A colony of a species of *Favia*, photographed in daylight, with its polyps contracted and the tentacles hidden.

FIG. 3. The colony illustrated in fig. 2, photographed at night by flashlight, with the tentacles fully extended.

Both figures are about natural size.

Fig. 2.

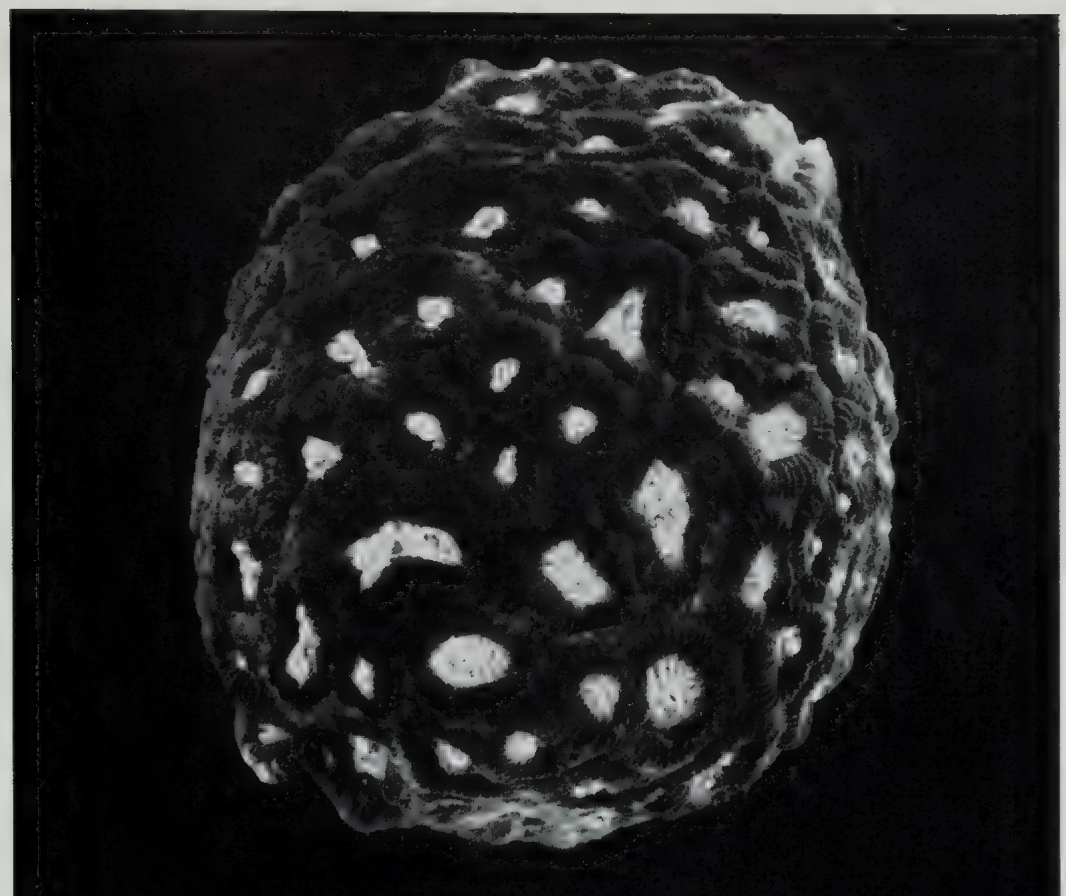

Fig. 3.

Photos T. A. Stephenson.] [*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE III.

Fig. 4. Massive corals, mainly species of *Favia* and *Coeloria*, exposed at low water spring tide on Michaelmas Island Reef, Inner Barrier series.

Fig. 5. Colony, probably of a species of *Coeloria*, exposed at low water spring tide on the seaward margin of the outer ridge on Ruby Reef, Outer Barrier series. The great size of this colony, which is fully exposed to the Pacific surf, is indicated by the adjacent crowbar, which is 3½ ft. long.

Photo M. J. Yonge.] FIG. 4.

Photo C. M. Yonge.] FIG. 5. [*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE IV.

FIG. 6.—Reef edge of North-west Island Reef, Capricorn Group, exposed during exceptionally low spring tides. The lithothamnion ridge (see Plate V, fig. 8) is seen in the background, and in the foreground the great wealth of species of *Acropora* which cover the living, outwardly growing, edge of the reef.

FIG. 7.—Colony of a species of *Montipora* photographed from overhead at low tide on Low Isles Reef and showing foliaceous type of growth found in sheltered waters.

Photo M. J. Yonge.]

FIG. 6.

Photo M. J. Yonge.]

FIG. 7.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE V.

FIG. 8.—View along the lithothamnion-covered reef crest at North-west Island Reef, Capricorn Group.

FIG. 9. Photograph, taken from overhead, showing encrusting growth of a wide variety of coral species in a shallow pool on the reef crest at North-west Island Reef.

Photo M. J. Yonge.]

FIG. 8.

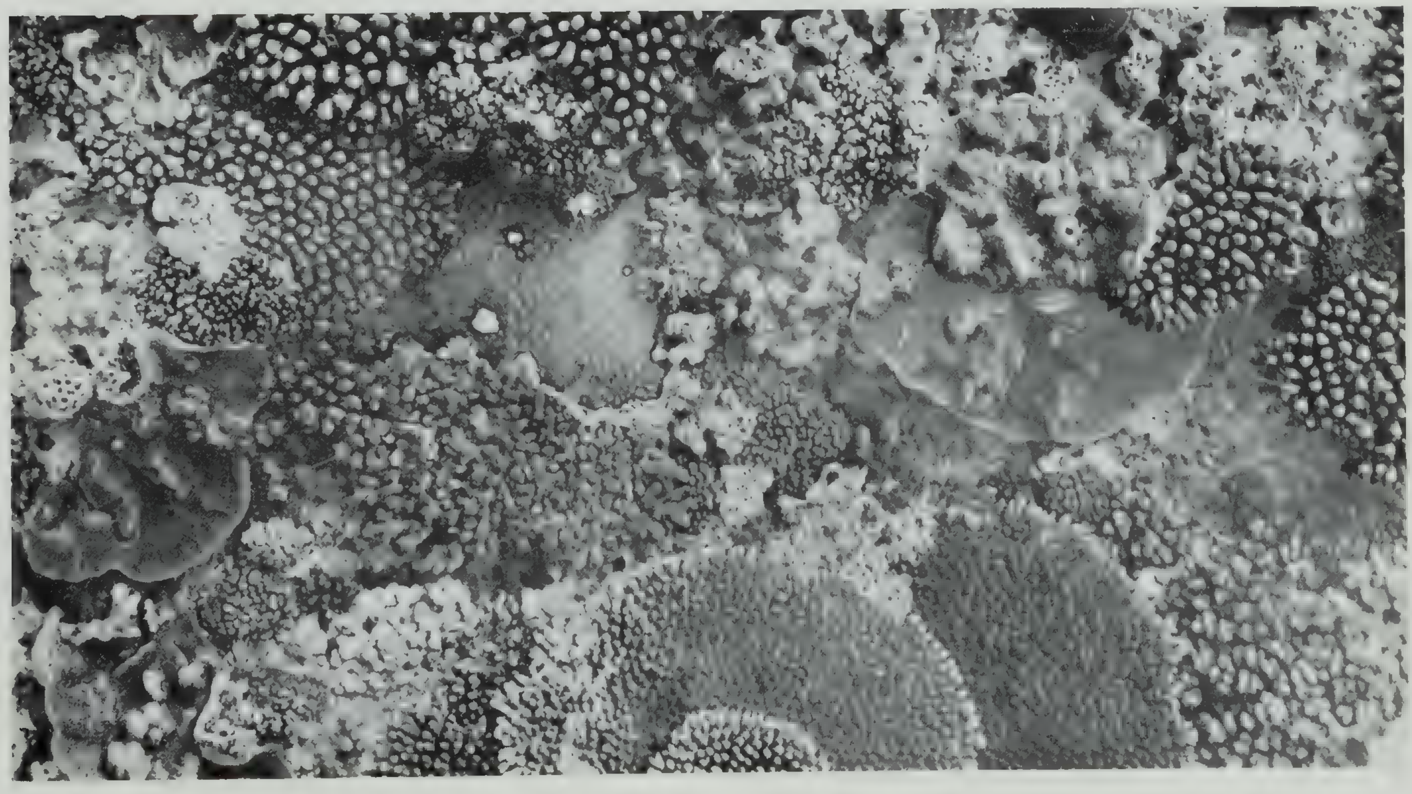

Photo M. J. Yonge.]

FIG. 9.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE VI.

Fig. 10.—Branching corals, largely species of *Acropora*, exposed during very low spring tides in the sheltered waters of the anchorage at Low Isles.

Fig. 11.—Photograph, taken from above, showing bracket-like colonies of *Acropora*, growing at the summit of a mushroom-topped pinnacle of coral rock in the lee of Pixie Reef, Inner Barrier series. The sandy bottom, characteristic of the lee of reefs, can be seen in the upper half of the photograph. It lies some 2 fathoms below the surface at low water.

Photo M. J. Yonge.]

FIG. 10.

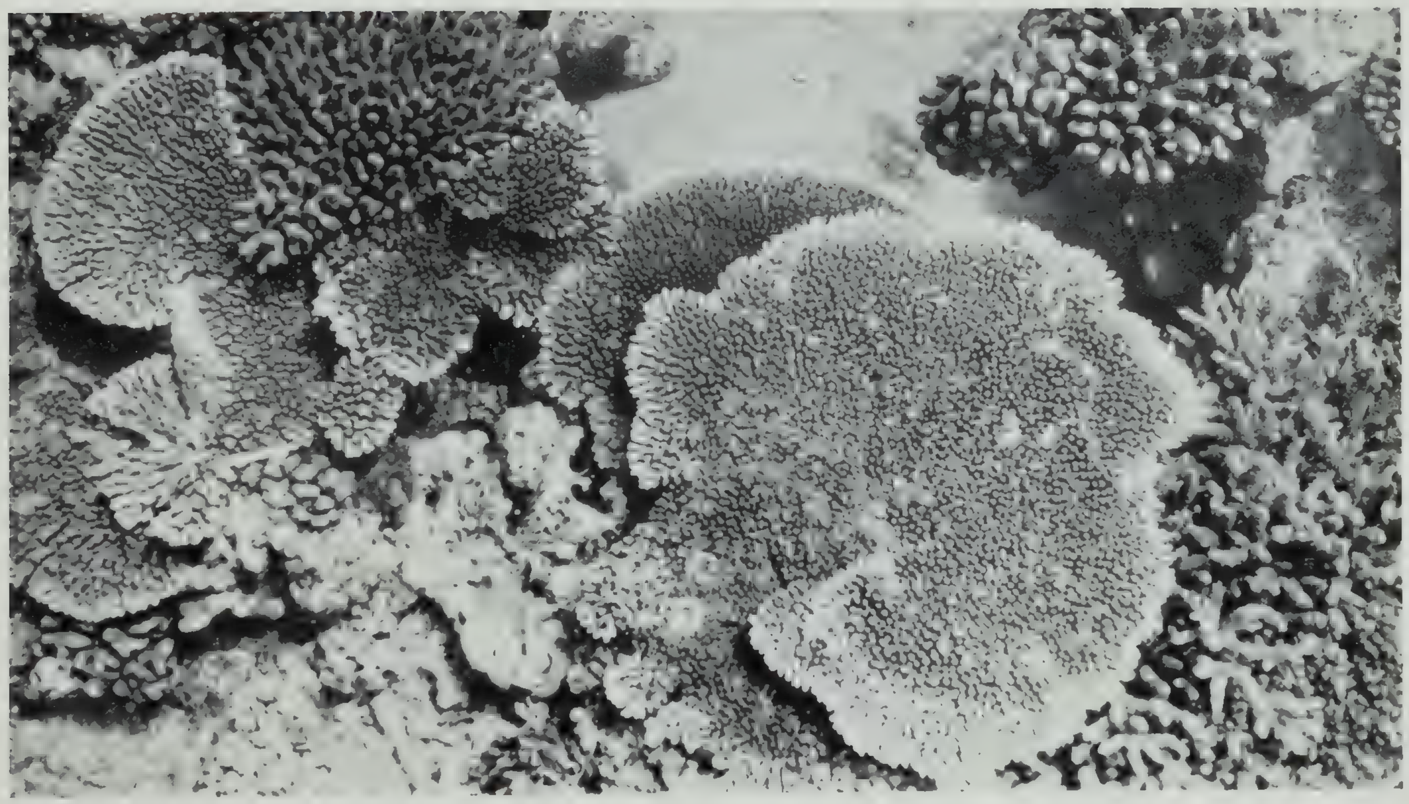

Photo M. J. Yonge.]

FIG. 11.

[*Adlard & Son, Ltd., Impr.*